42-N53p v.13
1914

W. G. FARLOW

THE

NEW PHYTOLOGIST,

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

IN CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

ASSISTANT-EDITOR:

F. CAVERS, D.Sc.

VOLUME XIII.

PP. VIII. AND 364.

WITH THREE PLATES AND NUMEROUS FIGURES IN THE TEXT

LONDON 1914

WILLIAM WESLEY & SON

28 Essex Street, Strand.

42
N53p
v.13
1914

Digitized by the Internet Archive
in 2018 with funding from
BHL-SIL-FEDLINK

https://archive.org/details/newphytologist1319tans

INDEX OF SUBJECTS.

Page

Absorption of Salts by Plants, The Antagonism between Ions in the—W. Stiles and Ingvar Jörgensen ... 253

Adaptations (see Xerophytic).

Adelaide, South Australia, Notes on the Flora around (Plates I and II and 3 Text-figs.) [Sketches of Vegetation at Home and Abroad. VIII]—T. G. B. Osborn 109

America, The International Phytogeographic Excursion in (1913)—A. G. Tansley 30, 83, 268, 325

Anatomy of *Stangeria paradoxa*, Notes on the (11 Text-figs.) —A. S. Marsh 18

Antagonism between Ions in the Absorption of Salts by Plants, The—Walter Stiles and Ingvar Jörgensen 253

Bacteria, A Contribution to the Physiology of the Purple Sulphur—Macgregor Skene 1

Batrachospermum, Notes on (10 Text-figs.)—S. Reginald Price 276

Biology of *Fegatella conica*, Note on the (1 Text-fig.)— A. C. Maybrook 243

Biotic Succession, A Study in (see White Moss Loch).

British Flagellates, Notes on, I-IV (3 Text-figs.)—F. E. Fritsch 341

Bryophytes in Relation to Habitat, Xerophytic Adaptations of (3 Text-figs.)—W. Watson 149, 181

Chondriosomes (Mitochondria) and their Significance [Notes on Recent Literature]—F. Cavers ... 96, 170

Cilia in Living *Volvox*, Demonstration of [Laboratory Note]—S. R. Price 324

Cyanophyceæ, A Method of Staining [Laboratory Note] —R. C. McLean 71

Cycadites and *Pseudocycas*, On the Relation between (Plate III and 1 Text-fig.)—Ruth Holden 334

Cycads, Pteridosperm Anatomy and its Relation to that of the (20 Text-figs.)—N. Bancroft 41

Desert Basin (see Salton Sea).

Electrical Conductivity as a Method of Investigation in Plant Physiology, The Measurement of (5 Text-figs.)—Walter Stiles and Ingvar Jörgensen ... 226

Evolution (see Monocotyledons).

Fegatella conica, Note on the Biology of (1 Text-fig.)—Annie C. Maybrook... 243

Fern-like Stem described by Count Solms-Laubach, A new [Note on Recent Literature]—I. M. P. Browne 93

Flagellates (see British).

"Fruiting Male" of *Phœnix dactylifera* L., Note on the (5 Text-figs.)—H. Martin Leake 69

Hirneola Auricula-judæ Berk. ("Jew's Ear") Further Observations on (9 Text-figs.)—M. J. Le Goc ... 122

International Phytogeographic Excursion (I.P.E.) in America (1913), The—A. G. Tansley ...30, 83, 268, 325

Ions (see Antagonism).

"Jew's Ear" (see *Hirneola*).

LABORATORY NOTES:—

I—R. C. McLean. A Method of Staining Cyanophyceæ 71

II—S. Reginald Price. Demonstration of Cilia in Living *Volvox* 324

Liverworts (see West-Himalayan).

Measurement of Electrical Conductivity as a Method of Investigation in Plant Physiology, The (5 Text-figs.)—Walter Stiles and Ingvar Jörgensen ... 226

Method of Staining Cyanophyceæ [Laboratory Note]—R. C. McLean 71

Mitochondria (see Chondriosomes).

Monocotyledons, Review of Literature concerning the Evolution of—N. Bancroft 285

Morphological and Biological Notes on New and Little Known West-Himalayan Liverworts—Shiv Ram Kashyap:—

I—(4 Text figs.) 206

II—(8 Text-figs.) 308

Note on the "Fruiting Male" of *Phœnix dactylifera* L. (5 Text-figs.)—H. Martin Leake 69

Notes on British Flagellates. I-IV (3 Text-figs.)—F. E. Fritsch 341

Page

Notes on the Anatomy of *Stangeria paradoxa* (11 Text-figs.)—A. S. Marsh 18

Notes on *Batrachospermum* (10 Text-figs.)—S. Reginald Price 276

Observations on *Hirneola Auricula-judæ* Berk. ("Jew's Ear") (9 Text-figs.)—M. J. Le Goc 122

Paléontologie Végétale, by F. Pelourde [Review]—H. H. Thomas 250

Phœnix dactylifera L., Note on the "Fruiting Male" of (5 Text-figs.)—H. Martin Leake 69

Photosynthesis, Pioneer Investigators of—R. J. Harvey Gibson 191

Physiology of the Purple Sulphur Bacteria, A Contribution to the Physiology of the—Macgregor Skene ... 1

Phytogeographic Excursion (see International).

Pioneer Investigators of Photosynthesis—R. J. Harvey Gibson 191

Plant Physiology (see Measurement of Electrical Conductivity).

Porometer and Potometer, A Self-Recording (7 Text-figs.)—W. Neilson Jones 353

Potometer (see Porometer).

Pseudocycas (see *Cycadites*).

Pteridosperm Anatomy and its Relation to that of the Cycads (20 Text-figs.)—N. Bancroft 41

Purple Sulphur Bacteria, A Contribution to the Physiology of the—Macgregor Skene 1

RECENT LITERATURE, NOTES ON :—

I—A New Fern-like Stem, described by Count Solms-Laubach—I. M. P. Browne... ... 93

II—Chondriosomes (Mitochondria) and their Significance—F. Cavers 96, 170

Relation between *Cycadites* and *Pseudocycas*, On the (Plate III and 1 Text-fig.)—Ruth Holden ... 334

Review of Literature Concerning the Evolution of Monocotyledons—N. Bancroft 285

Reviews :—
- I—The Flora of South Africa, by Dr. R. Marloth —W. C. W(orsdell) 107
- II—The Salton Sea : A Study of the Geography, Geology, Floristics and Ecology of a Desert Basin, by D. T. MacDougal and Collaborators —F. Cavers 280
- III—Paléontologie Végétale, by F. Pelourde—H. H. Thomas 250

Salton Sea, The : A Study of the Geography, Geology, Floristics and Ecology of a Desert Basin, by D. T. MacDougal and Collaborators [Review]—F. Cavers 280

Self-Recording Porometer and Potometer, A (7 Text-figs.) —W. Neilson Jones 353

Sketches of Vegetation at Home and Abroad :—
- VIII—Notes on the Flora around Adelaide, South Australia (Plates I and II and 3 Text-figs.) —T. G. B. Osborn 109

South Africa, The Flora of, by Dr. R. Marloth [Review]—W. C. W(orsdell) 107

Stangeria paradoxa, Notes on the Anatomy of (11 Text-figs.)—A. S. Marsh 18

Stellaria graminea, Variability in (2 Text-figs.)—A. S. Horne 73

Variability in *Stellaria graminea* (2 Text-figs.)—A. S. Horne 73

Volvox, Demonstration of Cilia in Living [Laboratory Note]—S. R. Price 324

West-Himalayan Liverworts, Morphological and Biological Notes on new and little known—Shiv Ram Kashyap :—
- I—(4 Text-figs.) 206
- II—(8 Text-figs.) 308

White Moss Loch, The : A Study in Biotic Succession (2 Text-figs.)—J. R. Matthews 134

Xerophytic Adaptations of Bryophytes in Relation to Habitat (3 Text-figs.)—W. Watson 149, 181

INDEX OF AUTHORS.

Page.

Bancroft, N. A Review of Literature concerning the Evolution of Monocotyledons ... 285

Bancroft, N. Pteridosperm Anatomy and its Relation to that of the Cycads (20 Text-figs.)... 41

Browne, I. M. P. A new fern-like stem described by Count Solms-Laubach [Notes on Recent Literature] 93

C(avers), F. The Salton Sea: a Study of the Geography, the Geology, the Floristics and the Ecology of a Desert Basin, by D. T. MacDougal and Collaborators [Review] 280

Cavers, F. Chondriosomes (Mitochondria) and their Significance [Notes on Recent Literature] 96, 170

Fritsch, F. E. Notes on British Flagellates. I-IV (3 Text-figs.) 341

Gibson, R. J. Harvey. Pioneer Investigators of Photosynthesis 191

Holden, Ruth. On the Relation between *Cycadites* and *Pseudocycas* (Plate III and 1 Text-fig.) 334

Horne, A. S. Variability in *Stellaria graminea* (2 Text-figs.) 73

Jones, W. Neilson. A Self-Recording Porometer and Potometer (7 Text-figs.) 353

Jörgensen, Ingvar and Stiles, Walter. The Measurement of Electrical Conductivity as a Method of Investigation in Plant Physiology (5 Text-figs.) 226

Jörgensen, Ingvar and Stiles, Walter. The Antagonism between Ions in the Absorption of Salts by Plants 253

Kashyap, Shiv Ram. Morphological and Biological Notes on new and little known West-Himalayan Liverworts:—
  I (4 Text-figs.) 206
  II (8 Text-figs.) 308

Leake, H. Martin. Note on the "Fruiting Male" of *Phœnix dactylifera* (5 Text-figs.) ... 69

Le Goc, M. J. Further Observations on *Hirneola Auricula-judæ* Berk. ("Jew's Ear") (9 Text-figs.) 122

Page

McLean, R. C. A Method of Staining Cyanophyceæ [Laboratory Note] 71

Marsh, A. S. Notes on the Anatomy of *Stangeria paradoxa* (11 Text-figs.) 18

Matthews, J. R. The White Moss Loch: a Study in Biotic Succession (2 Text-figs.) ... 134

Maybrook, Annie C. Note on the Biology of *Fegatella conica* (1 Text-fig.) 243

Osborn, T. G. B. Sketches of Vegetation at Home and Abroad. VIII—Notes on the Flora around Adelaide, South Australia (Plates I and II and 3 Text-figs.) ... 109

Price, S. Reginald, Notes on *Batrachospermum* (10 Text-figs.) 276

Price, S. Reginald. Demonstration of Cilia in living *Volvox* [Laboratory Notes] ... 324

Skene, Macgregor. A Contribution to the Physiology of the Purple Sulphur Bacteria ... 1

Stiles, Walter and Jörgensen, Ingvar. The Antagonism between Ions in the Absorption of Salts by Plants 253

Stiles, Walter and Jörgensen, Ingvar. The Measurement of Electrical Conductivity as a Method of Investigation in Plant Physiology (5 Text-figs.) 226

Tansley, A. G. The International Phytogeographic Excursion (I.P.E.) in America, 1913 ... ... 30, 83, 268, 325

Thomas, H. H. A New Book on Palæobotany (Paléontologie Végétale, by F. Pelourde) [Review] 250

Watson, W. Xerophytic Adaptations of Bryophytes in Relation to Habitat (3 Text-figs.)... 149, 181

W(orsdell), W. C. "The Flora of South Africa," by Dr. R. Marloth [Review] 107

THE
NEW PHYTOLOGIST.

VOL. XIII, NOS. 1 & 2. JAN. & FEB., 1914.
[PUBLISHED FEBRUARY 25TH, 1914.]

A CONTRIBUTION TO THE PHYSIOLOGY OF THE PURPLE SULPHUR BACTERIA.

BY MACGREGOR SKENE, B.SC.,
Lecturer on Vegetable Physiology, Aberdeen University.

UNDER the name "Sulphur Bacteria" we include a number of forms which in appearance and in mode of life stand far apart. They have one characteristic in common: all are capable of oxidising sulphur or one of its unoxidised compounds, producing in some cases sulphur, in others sulphuric acid. Two series may be distinguished. To the first belong those forms which are morphologically similar to ordinary bacteria, and which do not store up sulphur internally. Such are the *Thiobacilli* which have been described by Nathansohn (1902) Beijerinck (1904) and Lieske (1912 *a* and *b*). They oxidise thiosulphates to sulphur or sulphuric acid, and so obtain energy which they expend on the reduction of carbon dioxide, by this means gaining the possibility of leading an autotrophic life. The second series includes a number of forms which exhibit remarkable morphological peculiarities. They oxidise hydrogen sulphide to sulphuric acid—a process which takes place in two stages: sulphur is first formed, and is stored inside the cells in large globules, which are then further oxidised. This storage of sulphur lends the bacteria a very characteristic appearance. Moreover most of the organisms in question are very large, and live united in colonies or in filaments.

Here we can distinguish two sub-classes. The first consists of colourless forms. Of these two—*Beggiatoa* and *Thiothrix*—have been investigated quite recently from the physiological standpoint by Keil (1912); both have proved to be autotrophic. Finally we have those sulphur bacteria which possess a red pigment—the so-called *Purple Sulphur Bacteria*.

These are found in stagnating water, but are not very common. Since, however, they sometimes occur in such masses that they colour the water or the mud bright red, it is not surprising that they were early discovered and described; see Morren (1841), Cohn (1875), Ray Lankester (1873, 1876), Warming (1875). But it was only in the year 1888 that Winogradsky recognised the importance of the sulphur inclusions for their metabolism, and so laid a sure foundation for further investigations. At the same time he cleared up in essentials the systematics of this difficult group.

In order to study the life-histories of the different purple bacteria the Russian investigator devised a method by means of which he could keep the organisms in question under microscopical control for a considerable length of time. He placed small colonies in a drop of sulphuretted hydrogen water on a slide, and covered them with a slip, under which lay a few glass splinters to prevent crushing. If care was taken to prevent evaporation, and to add fresh sulphuretted hydrogen water once or twice every day, the bacteria throve for months, and multiplied considerably.

In spite of many endeavours Winogradsky was unable to obtain pure cultures, and therefore was obliged to draw his conclusions as to the nutrition of the bacteria from the results of his drop cultures. The chief points of his discussion may be summarised as follows:—

1. Hydrogen sulphide is absolutely necessary for a good growth: it is oxidised first to sulphur, then to sulphuric acid: the sulphur globules which one sees in the interior of the cells are the intermediate products of this oxidation: they grow in size if the supply of hydrogen sulphide is abundant, in absence of this gas they grow smaller and finally disappear.

2. In order to carry out this oxidation the bacteria require oxygen, but only in small quantities. In natural conditions they are always accompanied by minute green bacteria: these are capable of photosynthesis, and the oxygen so liberated is utilised by the sulphur bacteria, which are thus to be regarded as microaërophil.

3. The bacteria require organic food substances, but can flourish with quite small quantities: thus Winogradsky used for his cultures Strassburg tap water to which he added 0·005—0·01% of calcium butyrate, or of sodium acetate: with peptone and meat extract he could obtain no better results. This remarkable fact is to be explained (*a*) by the very slow growth of the bacteria, which

require a day or more for a single division, and (*b*) because the organic food substances are used only for body-building, energy being supplied solely by the oxidation of the hydrogen sulphide.

Since Winogradsky three investigators have busied themselves with the subject. Engelmann (1888), using his well-known "bacterium method," endeavoured to show that the sulphur bacteria give off oxygen in light. He considered that he had succeeded in doing so, and consequently held that sulphur bacteria were capable of photosynthesis, and that their red pigment played a part corresponding to that of chlorophyll in the higher plants.

His conclusions and his experimental data have been attacked from two sides. Winogradsky himself regarded them as improbable for purely theoretical reasons. Molisch (1907), in a monograph on *Purple Bacteria*, reinvestigated the question experimentally, and could not confirm Engelmann's results.

It is somewhat difficult to form an opinion on the part of Molisch's book which touches on the sulphur bacteria. He deals not only with the purple *sulphur* bacteria, but also with a number of others, which seem to have only the possession of the pigment in common with the hydrogen sulphide oxidising organisms. He obtained pure cultures of several species (*Rhodobacillus*, *Rhodobacterium*, etc.), which do not have the property of storing up sulphur globules. These thrive in solutions of organic food substances (1% peptone + 1% dextrine), grow better in light than in darkness, require no hydrogen sulphide, and are microaërophil.

He makes but few references specially to the sulphur-storing forms; but remarks that *Chromatium* grows well in the peptone-dextrine solution, and shows only a very slight development, if any, without peptone. But it must be added that on reading through his book, one has the impression that Molisch believes the sulphur bacteria to behave as do the other purple forms—that is, that they require organic food substance, and do not require hydrogen sulphide.

Finally, there must be mentioned a paper by Nadson (1903). From the results of one or two raw cultures he comes to the conclusion that hydrogen sulphide is unnecessary, and that in nature it serves only as a protection against oxygen. His experiments are few in number, and as they deal chiefly with bacteria showing no sulphur inclusions (only in one case were scanty granules observed), it is doubtful whether his conclusions can be applied to the sulphur bacteria in general.

When one considers these different views, one must admit that the results of Winogradsky are still the most worthy of attention. Although he worked with drop cultures only, he obtained a very clear insight into the necessities of the organisms he studied. Nevertheless the problem cannot be regarded as solved. Only *pure cultures* permit of a complete comprehension of the physiology of nutrition of micro-organisms. Pure cultures have unfortunately not yet been obtained; in the following paper, however, I wish to describe the results of experiments with, and of observations on mixed cultures, which may help in some degree to extend our knowledge of the physiology of the purple sulphur bacteria.

I—MATERIAL AND CULTURE METHODS.

Purple sulphur bacteria may be easily obtained, and cultivated under more or less natural conditions. According to Winogradsky it is only necessary to place pieces of *Butomus* rhizome in a deep glass vessel, fill up with water, and add some calcium sulphate, in order to obtain in the course of a few weeks a fine development of purple bacteria on the walls of the vessel: the appearance of the purple zooglœa is always preceded by a considerable evolution of hydrogen sulphide. I found this method to answer well in Strassburg[1]; but it failed when I tried it in Aberdeen. Consequently most of my experiments were carried out with sulphur bacteria from the salt-marshes near Kiel, material of which was very kindly sent me by Professor Dr. E. Lehmann, to whom I am much indebted. The water of these marshes contains 0·6% sodium chloride, but I found that the bacteria grew perfectly in water containing 2·7%, and all my culture solutions contained that quantity[2]. A continuous abundant supply of material is easy to maintain. A large (3 litre) wide-mouthed bottle is filled with salt water, to which is added about 30 grms. of chalk and 5 to 10 grms. of calcium sulphate: a few lumps of *Enteromorpha* are thrown in, and the liquid is innoculated with the sulphur bacteria. Hydrogen sulphide is rapidly produced by the reduction of the calcium sulphate, and probably also by the putrefaction of the *Enteromorpha*, and, if the bottle be placed in the light, a vigorous development of sulphur bacteria takes place in from two to four weeks according to the season. The zooglœa is thick, opaque, and of a fine red-purple colour. With such cultures one can observe the more rapid growth at the side of the vessel which is turned to the light, but not much more. It was therefore necessary to find some method, allowing of culture under conditions which could be controlled more exactly.

---

[1] Where Winogradsky's research was carried through.

[2] As that happened to be the concentration in the raw culture most suitable for using as infection material when I started my decisive cultures.

In the first place I tried drop cultures such as Winogradsky used: these have unfortunately many disadvantages. A great deal of time is occupied by their examination: each one must be "fed" with sulphuretted hydrogen water at least once every day: and when all is done it is impossible to control exactly the supply of food substance. Such cultures have scarcely given useful results.

I then tried cultures in conical flasks. A few bubbles of hydrogen sulphide were passed into each flask every day. This supply is however too uncertain, and too difficult to regulate. But with a modification of the method I attained my end, and was able to cultivate the bacteria under approximately known conditions.

I placed the conical flasks under a glass bell, which was fixed with wax and lard to a glass plate: the tubulus of the bell was provided with a double-bored stopper, through which passed two glass tubes: these could be closed by rubber tubing and glass stoppers. The tubes served for the admission of the necessary sulphuretted hydrogen. If such a bell of 3 litres content be provided with 50 to 150 ccs. of sulphuretted hydrogen (the measuring out of the gas was performed by a suitable piece of apparatus, into the details of which it is scarcely necessary to go) it takes several days before oxidation is complete. In general 50 to 100 ccs. were introduced into the bell to start with, and on the following days the contents tested by means of a small hand bellows, and lead acetate paper. When the reaction for sulphuretted hydrogen was given only very faintly, or not at all, then the gas supply was renewed. This renewal took place as a rule every second or third day. The method appears at first sight very rough, but in practice it gives excellent results. The bacteria developed as surely, and as rapidly as under the most favourable natural conditions.[1]

As regards the species which have been investigated it must be remarked that in the original infection material (from Kiel) many of the colonial forms described by Winogradsky were observed: the motile forms were all swarming conditions of these —typical *Chromatium* was not seen. In my raw cultures *Lamprocystis roseo-persicina*, formed the chief constituent of the

[1] The first culture I made with this method is dated 13th July, 1912—that is about six months before the description of a similar method for *Beggiatoa*, by Keil (1912).

red zooglœa: it was accompanied by abundant *Amœbobacter roseus:* less plentiful were *Thiopolycoccus ruber* and *Thiothece gelatinosa.* In the conical flasks on the other hand *Amœbobacter roseus* was always most abundant, being accompanied chiefly by *Lamprocystis roseo-persicina.* The following observations should therefore be taken to apply to *Amœbobacter.*

II—The Food Requirements of the Purple Sulphur Bacteria.

As has already been remarked Winogradsky expressed the opinion that the purple sulphur bacteria required organic food-substance, but only in minimal quantities: in his drop cultures he used Strassburg tap water (which contains very little organic substance) to which he added 0·005%—0·01% calcium butyrate or sodium acetate: no better growth was obtained with peptone or beef extract. Molisch on the other hand maintains that *Chromatium* will only grow in solutions containing 1% peptone + 1% dextrine. Apart from these unsatisfactory, and contradictory statements, there is to be found in the sulphur bacteria literature absolutely nothing on the question of food requirements.

In order to determine the best conditions for the development of the bacteria, I carried out a long series of comparative cultures in different nutrient solutions, and I can fully confirm Winogradsky's statements, in so far that I could never observe the slightest improvement in the growth of the bacteria resulting from the addition of organic compounds.

It may be stated at once that the quickest and most vigorous development took place when the bacteria were provided with a solution, the constitution of which differed only slightly from that employed by Lieske (1911), for the culture of the *Iron Bacteria:* it had the following constitution:—

Ammonium sulphate	0·75 grms.
Magnesium sulphate	0·05 ,,
Potassium dihydrogen phosphate ...	0·05 ,,
Potassium chloride	0·05 ,,
Calcium nitrate	0·01 ,,
Sodium chloride	27·0 ,,
Calcium carbonate	10·0 ,,
Distilled water	1000 ccs.

If a small conical flask (50 to 100 ccs.) be provided with as much of this solution as forms a layer 1 to 1½ cms. deep (the chalk of course forms a sediment), be infected with sulphur bacteria, and placed in the sulphuretted hydrogen atmosphere, then in the course of 10 to 30 days, according to the season of the year[1], a vigorous development of the bacteria takes place. The chalk sediment becomes covered with a rich red-purple zooglœa.

SOURCE OF NITROGEN.

The following substances were tested :—

Egg albumen.
Peptone.
Asparagine.
Glycocoll.
Urea.
Ammonium nitrate.
Ammonium sulphate.
Calcium nitrate.

These substances were employed in a concentration of 0·08% in addition to the mineral constituents of Lieske's solution, less of course the ammonium sulphate. As a control cultures without nitrogen were infected. The egg albumen was added in the form of lumps of boiled white of egg. The necessary salt and chalk were added. For each culture a flask and two test tubes were used.

After three weeks, the result was that the growth in ammonium sulphate was best: albumen, peptone and asparagine were only slightly less favourable: a slight development was observed in urea: in glycocoll, ammonium nitrate, and calcium nitrate no growth had taken place. One might conclude from this, that peptone, asparagin and albumen formed as satisfactory sources of nitrogen as ammonium sulphate. When, however, the various solutions were tested with Nessler's Reagent, at the end of the experiment, it was found that these three gave almost as strong a reaction as the ammonium sulphate; further that urea gave a slight reaction ; while glycocol—and of course calcium nitrate—gave negative results. This must be referred to a production of ammonia from the various compounds in question under the action of other bacteria which are present in these mixed cultures: ammonium nitrate appears to be strongly toxic.

The same series of nitrogenous compounds was tried with 0·25% solutions of calcium lactate and of mannite: the results were quite similar, except that throughout the growth was less vigorous.

---

[1] The varying of the rate of development with the change of the season depends on the amount of light available, and is not concerned with temperature changes.

To determine the most suitable concentration of ammonium sulphate, cultures with different concentrations of that salt were employed, namely :—0 : 0·01% : 0·05% : 0·1% : 0·25% : 0·5%.

In the first and last of these no growth took place : the other solutions all showed a more or less satisfactory development, but in that containing 0·1% the growth was best.

The conclusion which may be drawn from these experiments is that ammonium sulphate is the most favourable source of nitrogen for the purple sulphur bacteria : but that, as in mixed cultures a decomposition of certain organic compounds with formation of ammonium takes place, such compounds permit of a more or less satisfactory growth, so long as they do not otherwise exert a harmful influence. Such compounds are albumen, peptone and asparagine.

SOURCE OF CARBON.

The question of the source of carbon is much more difficult to decide. Pure cultures are even more desirable here than in dealing with the source of nitrogen. As I was unable to obtain these, I attempted, by means of comparative cultures, to give at all events a *probable* solution of the problem. Using 0·15% ammonium sulphate as the source of nitrogen I infected cultures containing the following substances :—

Potassium formate.
Potassium tartrate.
Calcium formate.
Calcium lactate.
Calcium butyrate.
Mannite.
Dextrose.
Maltose.
Control without organic compound.

Of each of these four different sets of cultures were carried out :—

(1) Organic compound 0·25% + ammon. sulph.
(2) „ „ 0·125% + ammon. sulph.
(3) „ „ 0·25% + full Lieske soln.
(4) „ „ 0·125% + full Lieske soln.

Of each of these either two or three cultures were infected. As the experiment was commenced in March, when the conditions are unfavourable, growth was rather slow. The chief results were as follows:—

1. In the cultures of the first two series at most only a slight growth was observed,[1] even after the lapse of four months.

2. In the cultures of series (3) and (4) a moderate development took place after one month only in the control solutions, without organic substances. A fortnight later the development in the control solutions was complete and vigorous, a slight development was observed in dextrose and maltose, and a very slight development in mannite. After four months the growth in dextrose, maltose, mannite and potassium formate was good, or very good: long before this the zoogloeæ of the control cultures were fully developed and had commenced to show signs of dying.

3. The growth is constantly better and quicker in the solutions with the lower concentration of organic substance.

A few other combinations were tried:—

Glycocoll + calcium formate (0·2%).
Glycocoll + calcium lactate (0·2%).
Asparagine mannite + (0·2%).
Urea + mannite (0·2%).
Peptone + mannite (0·2%).
" + glycerol (0·2%).
" + dextrose (0·2%).

And a decoction of *Enteromorpha*. Only in this last was a slight growth observed.

It would appear then that all these substances are without favourable influence on the development of the sulphur bacteria: rather would it seem that they tend to inhibit that development. It seems remarkable that precisely the most highly organised compounds permit of the best growth. It must be noted, however, that the growth is never so good as when only mineral substances are present, that it only takes place if these mineral substances are added, that the maximum of development occurs about two months later than in pure mineral solutions, and that the lower the concentration the better is the growth. Perhaps it may be assumed that precisely these substances will, in mixed cultures, be most rapidly attacked by other micro-organisms, and decomposed so far as to destroy their inhibiting influence.

If now it be the case that the purple sulphur bacteria grow best in solutions containing no organic compounds, it might well be thought that they are *autotrophic*. When I used one of these flask cultures for infecting Lieske's solution, I obtained a good growth in the second generation: the third generation was equally satisfactory. That such a strong development could take place at the expense of the small amounts of organic material carried over with the infection, or of dust particles from the air, I do not think possible. Thus it would seem logical to infer an assimilation of carbon dioxide in the culture flasks. But as we are dealing with mixed cultures it does not by any means follow that the assimilation is carried out by the purple sulphur bacteria. In the present case the matter is complicated by the fact, that in my cultures an undoubted autotrophic bacillus is always present. After one or two weeks there constantly appears on the surface of the liquid a thick whitish or yellow skin, which consists of sulphur, the oxidation product of a minute bacillus oxidising hydrogen sulphide. This bacillus (which is mentioned by Lieske, 1912 *a*) is easily isolated by means of silica jelly plates. It grows excellently in the solution employed for the purple bacteria, in presence of hydrogen sulphide, and produces a characteristic deposit on the surface of the liquid.

---

[1] Only with calcium lactate was the development more than very slight.

It is at all events a possibility that the carbon assimilation takes place solely through this organism, and that the purple forms live at its expense. A symbiosis in the strict sense of the word does not come into consideration: in the first place because the bacillus and the purple bacteria inhabit, in the main, different layers of the culture liquid: and in the second place because the bacillus does not require the others, and can live without them. Some looser connection, to the advantage of the purple forms, might, however, be quite possible. The solution of the problem can again be obtained only with pure cultures. Without these it was possible to try by comparative cultures, to find out in which direction the answer to the question lies.

Eight flasks were infected with a pure culture of the bacillus, and allowed to develope for 12 days: at the end of that time when all showed a vigorous development, four were sterilised in the steamer, and four fresh uninfected flasks were added. Of each of these three series three flasks were infected with purple sulphur bacteria, and one was left as a control. Growth began in all the infected flasks about the same time. After three weeks the development was estimated: the control flasks showed no growth: the others were all very nearly equal, such small differences as could be noted were in favour of those not previously infected with the bacillus, next came the sterilised, and finally those which were provided with a living bacterial flora. A second series gave precisely similar results.

From these experiments we may conclude that under the conditions in question the autotrophic bacilli have no favourable influence on the growth of the purple sulphur bacteria: the evidence is not conclusive, as a smaller number of the bacilli might be a necessary condition, but it has at least some probability and so cannot be left out of consideration.

SOME METHODS BY WHICH PURE CULTURES WERE SOUGHT TO BE OBTAINED.

The trials were chiefly concerned with the possibility of growth on solid substrata. Winogradsky (1888) remarks that growth does not take place on gelatine, but does not enter into details: in particular be does not mention the culture media employed, nor whether he supplied sulphuretted hydrogen to his cultures—only that in gelatine the sulphur bacteria perish rapidly. It was therefore advisable to investigate as many solid media as possible:—

1. Agar + Lieske's solution.
2. Agar + peptone 0·5% + dextrose 0·5%.
3. Gelatine + Lieske's solution.
4. Gelatine + Enteromorpha extract.
5. Silica jelly + Lieske's solution.
6. Plaster of Paris + Lieske's solution.
7. Filter paper + Lieske's solution.

All received the requisite quantities of salt and chalk: nos. 1-5 were infected by painting the surface and also in the usual manner by pouring plates. Hydrogen sulphide was supplied as usual. Unfortunately all these media gave negative results.

There are three possible explanations of this failure:—

1. The medium may contain too much organic substance (agar and gelatine): but this does not apply to nos. 5-7.

2. Neutralisation may be too slow, when the chalk is embedded in a jelly. Here we may remark that the diffusion of acid in a jelly is quite rapid. I was unable to replace the chalk by a soluble carbonate. Sodium bicarbonate and potassium carbonate appear to be toxic in small concentrations: 0·25% of the former was sufficient to inhibit growth almost completely.

It was found possible to grow the bacteria in flasks containing at the bottom a layer of agar 1 cm. thick, containing the chalk, on to which a layer of the culture solution was poured. Under these conditions separate colonies were formed on the surface of the agar: but at the same time the autotrophic bacillus grew completely over the jelly, and so rendered an isolation impossible. The experiment proves at least that the failure to grow in solid media is not due to difficulty in neutralisation.

3. There only remains the possibility of an unknown action of the solid medium as such. This view is supported by the fact that in two cases a slight growth was observed in solid media: the first was in gelatine at a spot where other organisms had caused liquefaction: the second in silica, where liquefaction had taken place as the result of jarring. The attempt to isolate the bacteria by chemotatic methods proved equally unsuccessful. It was made with fresh-water *Chromatium* material. It is not difficult to entice the Chromatia into a capillary by means of a solution of hydrogen sulphide of suitable strength, but unfortunately they are invariably accompanied by masses of two other organisms—a slender bacillus, and a long spirillum (cp. Lidforss, 1912).

REACTION OF THE LIQUID.

As to this, we may note that it must be slightly alkaline or at least neutral. This is more necessary even than with ordinary bacteria, because the metabolism of the sulphur bacteria entails the constant production of fairly large quantities of sulphuric acid: this must be neutralised or growth is inhibited. This is clearly shown by the fact that cultures not supplied with chalk show no development. The chalk cannot be replaced by magnesium carbonate.

III—THE RELATION OF THE PURPLE SULPHUR BACTERIA TO HYDROGEN SULPHIDE.

In spite of the fine reasoning of Winogradsky, Molisch and Nadson have cast doubts on the necessity of hydrogen sulphide for the sulphur bacteria: the latter says definitely that it only serves as a protection against oxygen. As the question could not be regarded as settled it was considered advisable to carry out cultures designed to investigate the relation of the bacteria to the gas in presence of which they always occur in nature. If flasks are infected with sulphur bacteria, and some are placed in the air, others under the bell-jars with hydrogen sulphide, it is found that only the latter show a (strong) development: the former show absolutely none. If in addition we use boiled air-free water, and seal the flasks with liquid paraffin, the result is exactly the same—no development occurs.

It was thought possible that the hydrogen sulphide might be replaced by sodium thiosulphate. The following scheme was carried out:—

0·5% Sodium thiosulphate + the usual salts
- in air
  - light
  - dark
- closed with paraffin
  - light
  - dark
- + 1% Potassium nitrate
  - air
    - light
    - dark
  - O
    - light
    - dark

All cultures gave a negative result.

Finally I tried a number of other sulphur compounds, to see if it were at all possible to replace the hydrogen sulphide:—

Sodium bisulphite.
Sodium sulphide.
Sodium thiosulphate.
Potassium sulphide.
Calcium sulphide.
Iron sulphide.

Of each 0·5% was added to the culture solution, and four different conditions were investigated:—

A a. Aërobic.
A b. Anaërobic (boiled water + paraffin).
B a. + 0·5% Potassium nitrate, aërobic.
B b. + 0·5% Potassium nitrate, anaërobic.

A few bubbles of hydrogen sulphide were added to each that the change might not be too sharp.

The results were throughout negative[1]; even after six weeks no trace of development was visible. The material that was used for infection gave a fine growth in a fortnight (August) under suitable conditions.

It may therefore be concluded with certainty, that the presence of a certain amount of hydrogen sulphide is absolutely necessary to the development of the purple sulphur bacteria.

---

[1] In one anaërobic thiosulphate culture a purple sulphur bacterium, which does not agree with any of Winogradsky's forms, appeared: it seems to come nearest *Rhabdochromatium*: the cause of this requires further investigation: there is the possibility of a production of hydrogen sulphide by reduction of the ammonium sulphate.

IV.—RELATION OF THE PURPLE SULPHUR BACTERIA TO LIGHT.

Engelmann (1888) Winogradsky (1888) and Molisch (1907) have investigated in detail the influence of light on the movements of *Chromatium* and other swarming forms: Englemann also observed that the growth in light is much better than in darkness. On this point Winogradsky is silent. Molisch states that his purple bacteria grow only in light, and erects for them a new physiological class of organisms, which can assimilate *organic* carbon only in presence of light.

To investigate this point I carried out several series of cultures which gave quite definite results. One set of cultures in the following media was placed in the light, another set in a carefully darkened cardboard box:—

1. Lieske's Solution.
2. „ „ + dextrose 0·15%.
3. „ „ + calcium lactate 0·15%.
4. „ „ + potassium formate 0·15%.
5. Ammonium sulphate 0·075% + dextrose 0·15%.
6. „ „ „ + calcium lactate 0·15%.
7. „ „ „ + potassium formate 0·15%.

After two to three weeks the light cultures in Lieske's solution showed a strong development: all the dark cultures were absolutely without growth.

It may be concluded that the sulphur bacteria require light for their development.

Further experiments with a view to studying the effects of the different parts of the spectrum were carried out under double bells containing the customary solutions, potassium bichromate, and copper sulphate + ammonia. As is well known these solutions do not give pure spectra. With bichromate it is possible to shut out all the blue rays without too seriously diminishing the light intensity: but with the copper-ammonia solution a complete exclusion of the red can only be obtained by sacrificing much of the blue as well. The blue solution was therefore chosen of a strength which permitted of the passage of a considerable quantity of red light.

In red light the bacteria grow very well, though not quite so quickly as in daylight. After three weeks (August) the development was only moderate, after a month it was very good. In blue light on the other hand it is much slower: after three weeks only traces of red are to be seen on the sediment: after a month development goes on more quickly, and after five to six weeks the development in the blue is as good as in the red. Whether this is to be referred to the action of the blue rays, or of such red rays as penetrate the filter, cannot be definitely stated. But in any case it is certain that if the red rays of ordinary daylight are not alone effective, at least they are much more so than are the blue.

For the sake of comparison I tested the two filters with *Elodea*, by means of the gas-bubble method. The relative photosynthetic activity of daylight: red: blue, was about 6 : 3 : 1.

Why light should be necessary for the development of the sulphur bacteria we are not yet in a position to say. If we had an exact demonstration of the capacity of the bacteria to assimilate carbon dioxide, we might well regard the action of light as being bound up with the process. But as the matter stands we cannot well build theories on the fact that red light is more effective than blue. It is also by no means certain that Bacteriopurpurin, the red pigment, is a true chromophyll.[1]

V.—THE RELATION OF OXYGEN TO THE PURPLE SULPHUR BACTERIA.

Different investigators have expressed very different views on the relation of the sulphur bacteria to oxygen. As already remarked Nadson regards them as anaërobic. Molisch and Winogradsky on the other hand consider that they require small quantities of oxygen.

As Winogradsky was able to show, in a convincing manner, that they continually carry on an oxidation of hydrogen sulphide to sulphur, and of sulphur to sulphuric acid, and that they carry out this oxidation in absence of any oxidising agent such as potassium nitrate, it seems to follow necessarily that they require a supply of oxygen. How this supply can be obtained, in situations where there is always present a considerable amount of sulphuretted hydrogen, is the problem.

Winogradsky observed that the forms with which he worked always lived in the neighbourhood of little groups of very small rods and cocci, which were bright green in colour. He believed that the photosynthetic activity of these resulted in the liberation of a sufficient quantity of oxygen to serve the needs of the sulphur

[1] Molisch's statements (1907) concerning Bacteriopurpurin, in so far as they may refer to *Amœbobacter* and *Lamprocystis*, are not exact: if a piece of zooglœa is placed in absolute alcohol then, whether the treatment is in heat or cold, a solution is obtained which is *brick- to purple-red*, and certainly not *green*. A separation of the Bacteriochlorin and the Bacteriopurpurin in this solution is readily carried out by capillary analysis. A drop of the solution placed on filter-paper forms a bright red patch with a narrow, sharply differentiated, bright green margin.

bacteria. When I was cultivating marine species I was unable to observe these green bacteria in a single case. Quite recently, however, I have had at my disposal very fine fresh-water material of *Chromatium Okenii* (for which my best thanks are due to Dr. O. V. Darbishire), and in this the green bacteria certainly do occur with great regularity. They are very small—about 1·7μ long and 0·5μ broad, and bright green: they occur in little spiny clumps, which cannot be mistaken for such forms as *Stichococcus*. If a *Chromatium* settles down it always does so beside one of these little green masses. It is therefore probable that Winogradsky's views are correct.

Amongst the salt-water forms I have never seen these green bacteria: instead, however, there is a frequent development of *Chlorella* and of several blue-green algæ. In my flask cultures these did not as a rule make an appearance—such flasks as showed a development of green algæ had of course to be rejected.

In nature, then, the purple sulphur bacteria obtain their supply of oxygen from green assimilating organisms in their neighbourhood. It is probable that in my flask cultures the method of supplying sulphuretted hydrogen, solved at the same time the problem of oxygen supply. In the bell-jars there is always present a large excess of oxygen, and as I generally waited until all traces of sulphuretted hydrogen had disappeared before renewing the supply, there must have been in the solution a constant varying between sulphuretted hydrogen and oxygen content. Under these conditions the bacteria certainly developed splendidly. It is also of interest, that when test-tubes were used instead of flasks, and the layer of liquid had a depth of 5 to 6 cms. instead of 1 to 2 cms., the development was in the first place rather slower, and, in the second took place on the walls of the test-tube near the surface of the liquid—not on the sediment at the bottom. I imagine that this is to be referred to the less easy penetration of oxygen to the lower layers.

That the bacteria are certainly not anaërobic is clear from the fact that they can remain alive for several days in a liquid exposed freely to the air.

The views of Molisch and Winogradsky, that a certain small quantity of oxygen is necessary, would seem to be well founded.

VI.—SUMMARY.

The results of the foregoing experiments may be summarised as follows:—

1. The attempts to obtain pure cultures of purple sulphur bacteria have been without success.

2. In mixed cultures *Amœbobacter* (and probably also *Lamprocystis*) thrives best in a mineral solution, containing ammonium sulphate as a source of nitrogen, and with chalk as a neutralising agent.

3. All the organic sources of nitrogen and carbon which were investigated, proved to be without favourable influence on the growth of the bacteria: on the contrary, as a rule, they tend to inhibit development.

4. A loose symbiosis with autotrophic thiobacilli is possible, but does not seem likely.

5. Development can only take place in presence of hydrogen sulphide: this cannot be replaced by other sulphur compounds.

6. Growth only takes place in light: red light is more effective than blue.

7. The purple sulphur bacteria require free oxygen which is probably supplied in nature by associated green organisms.

The investigation was commenced at the suggestion of Professor Dr. Ludwig Jost in Strassburg. It is a great pleasure to express my thanks to Professor Jost, for the help and criticism he has always placed at my disposal, both when I was in Strassburg, and since my return to Aberdeen.

LITERATURE.

1. Beijerinck, W. M., 1904. Bakt. Centr. Abt. II **11**, 593.
2. Cohn, F., 1875. Beitr. z. Biol. d. Pflanz. **1**, 141.
3. Engelmann, Th. W., 1888. Bot. Ztg. **46**, 661.
4. Keil, F, 1912. Beitr. z. Biol. d. Pflanz. **11**, 335.
5. Lankester, E. Ray, 1873. Quart. Journ. Microscop. Science **13**, 408.
6. ——— 1876. *Ib.* **16**, 27.
7. Lidforss, B., 1912. Ber. d. deutsch. bot. Ges. **30**, 262.
8. Lieske, R., 1911. Jahrb. f. wiss. Bot. **49**, 90.
9. ——— 1912 *a.* Sitzber. d. Heidelberger Akad. d. Wissenschaften, 63.
10. ——— 1912 *b.* Ber. d. deutsch. bot. Ges. **30** (12).
11. Molisch, Hans, 1907. Die Purpurbakterien (Jena).
12. Morren, C. H., 1841. Mém, de l'acad. de Bruxelles, p. 41.
13. Nadson, G., 1903. Bull. jard. imp. bot. St. Petersburg **3**, 91.
14. Nathansohn, A., 1902. Mitteil. aces. d. Zoolog. Stat. zu Neapel **15**, 655.
15. Warming, E., 1875. Om nogle ved Dänmarks Kyster levende Bakterier (Kjöbenhavn).
16. Winogradsky, S., 1888. Beiträge zur Morphologie u. Physiologie der Bakterien **1** (Leipzig).

NOTES ON THE ANATOMY OF *STANGERIA PARADOXA.*

By A. S. Marsh, B.A.,

Frank Smart Student, Gonville and Caius College; Senior Scholar, Trinity College, Cambridge.

[With Eleven Figures in the Text.]

Historical.

THE vegetative anatomy of *Stangeria* has been the subject, wholly or in part, of many previous papers. Kraus (2) described in some detail the histological characters of the leaf, and this account was amplified, with special reference to the course of the foliar bundles, by Nestler (4). The stem is described in a paper by Solms Laubach (8), but this deals chiefly with the vascular supply to the cone and the method of branching induced by cone-formation. The "mesarch" bundles of the leaves are discussed in a general paper on Cycad petioles by Le Goc (3), not yet published, but the manuscript of which the author has very kindly allowed me to read. The most complete description of the anatomy is given by Pavolini (5), but there seemed still a certain number of points to be cleared up, and with some of these the present paper attempts to deal.

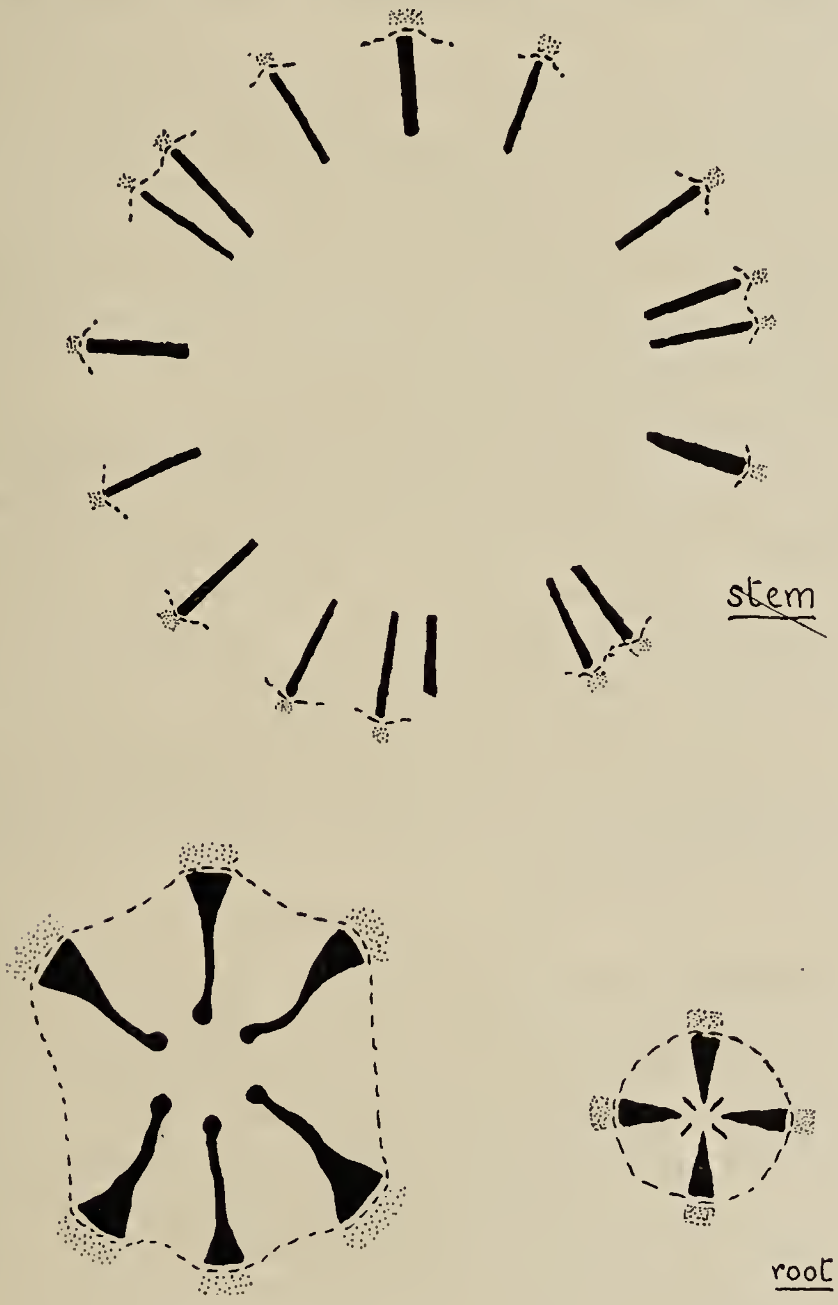
Material.

The material examined was chiefly a small stem with leaves attached, and a leaf with the adjoining portion of cortex. The former came from South Africa and was given me by Professor Seward, the latter was kindly supplied by Mr. Lynch, Curator of the Cambridge Botanic Garden.

The stem was 13·8 cm. long and 4·2 cm. in diameter at its thickest part. Below it tapered gradually into root and above it bore three leaves, the largest of which was 50 cm. from base to tip. Of this length, from the base to the insertion of the lowest pinnæ was 25·8 cm. and the terminal leaflet was 11·7 cm. long. Altogether there were 12 pinnæ arranged in approximately opposite pairs. The lateral pinnæ measured 14 to 16 cm. in length.

Stem Anatomy.

The stem is subterranean and there is little development of mechanical tissue. The cork is very thin and the single ring of wood is small and feebly developed, having a diameter of only 0·9 cm. at a point where the diameter of the stem was 3·7 cm. In transverse section one sees about 16 groups of tracheids, each group being 2 to 6 cells thick in a tangential direction and about a millimetre long radially. Beyond each group of tracheids, towards the periphery, is a phloem group separated from the xylem by cambium. Outside the phloem are first fibre-like cells with mucilaginous walls and then true mucilage cells. The rest of the stem, *i.e.*, the greater part of the tissue is composed of thin-walled storage parenchyma with much starch. In both cortex and medulla this is traversed by large mucilage canals and the cortex also



Base of Stem.

FIG. 1.—Diagrammatic Transverse Sections showing distribution of wood (black), phloem (dotted), and cambium (dotted line) in stem, both main portion and base, and in root.

contains the numerous bundles which supply the leaves. Just outside the stele the general parenchyma shows peculiar patches of tissue which, without having any obvious histological difference from the rest of the cortex, takes up rather more stain and which always remained cloudy in the cleared preparations made in investigating the course of the leaf-trace bundles ("cloudy tissue" of Fig. 1*).

In the main part of the stem, as described above, the cambium extends beyond each bundle laterally but is not continued unbroken all the way round. At the base of the stem, however, the cambium is continuous and the groups of tracheids are much fewer in number, much broader and extend further towards the centre of the stem. From this we pass to the root which has a tetrarch structure with continuous cambium and broad wedges of secondary wood opposite the phloem groups (see diagram Fig. 1).

The wood in the stem shows no sharp differentiation into primary and secondary portions, as except for the few small annular protoxylem elements, the whole of the wood is composed of tracheids, generally hexagonal in cross section, with a rather open type of scalariform pitting (see Fig. 7). The tracheids may even appear annular or slightly reticulate rather than scalariform. No trace of ordinary bordered pitting was found anywhere in the plant.

The stem wood is uniformly endarch and no trace could be seen of medullary bundles or of accessory zones ("abnormal zones") described in many Cycads.

THE GIRDLE SYSTEM.

This was investigated by cutting thick sections (about 3 mm.) and clearing them with *Eau de Javelle.* They were then stained with fuchsin, washed first with dilute acetic acid and then with water, taken through increasing strengths of alcohol and finally cleared with xylol. In this way it was possible to trace with great accuracy the course of the bundles supplying each leaf-base.

Stangeria shows an interesting variation from the normal type of Cycad girdle-trace. Ten leaf-supplies were traced through the cortex and eight of these were found to consist of a typical girdle, plus four strands running directly from the main ring to the leaf-base (Figs. 2 and 3). There are thus six main strands supplying the leaf, but each of these may branch at any point, though often a bundle branches only for the two resultant strands to reunite. At the base of the leaf (usually difficult to see when the leaf has fallen and the stem has swollen by growth) is a complex system of branches and anastomoses resulting in a ring of about nine bundles entering the petiole.

The two atypical cases, both of which were near the top of the stem were (1) a girdle with only two accessory bundles from the main ring, and (2) a leaf-supply consisting of three bundles coming straight from the stem stele and branching only on the side towards the leaf-base (Fig. 4).

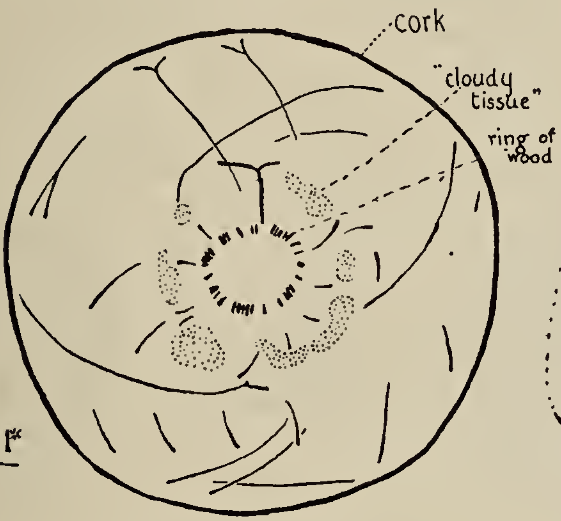


Fig. 1*

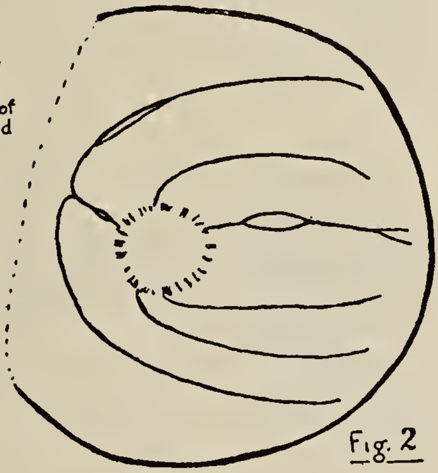


Fig. 2

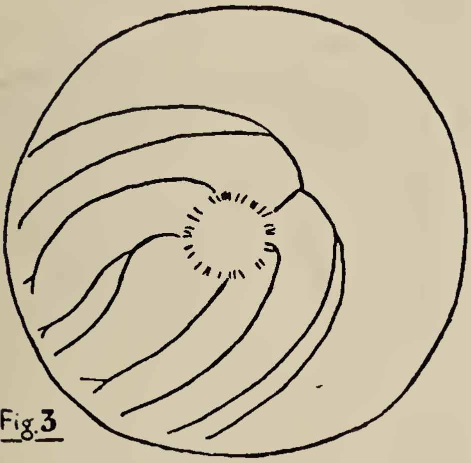


Fig. 3

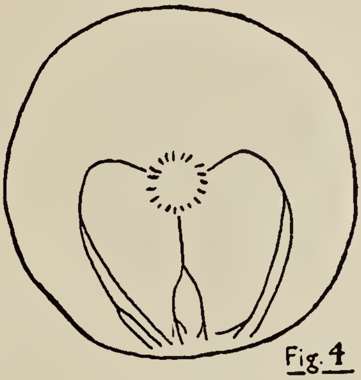


Fig. 4

FIG. 1*.—Thick section of *Stangeria* stem, cleared and stained, showing leaf-trace bundles in the cortex. (N.B.—The thicker a line the nearer to the top of the section is the bundle which it represents).

FIGS. 2 and 3.—Normal type of vascular supply to leaf.

FIG. 4.—One of the two abnormal leaf-trace systems.

The leaf-bases are only slightly above the point of issue of the bundles from the central cylinder so that, the stem being fairly thick, the bundles pass out almost horizontally, but the internodes being very short, one sees in any transverse section, bundles of two or three leaf-systems (Fig. 1*).

These bundles in the cortex were seen in section to be made up of centrifugal xylem and phloem often accompanied by mucilage canals. An obvious cambium is present and the wood is probably mostly secondary.

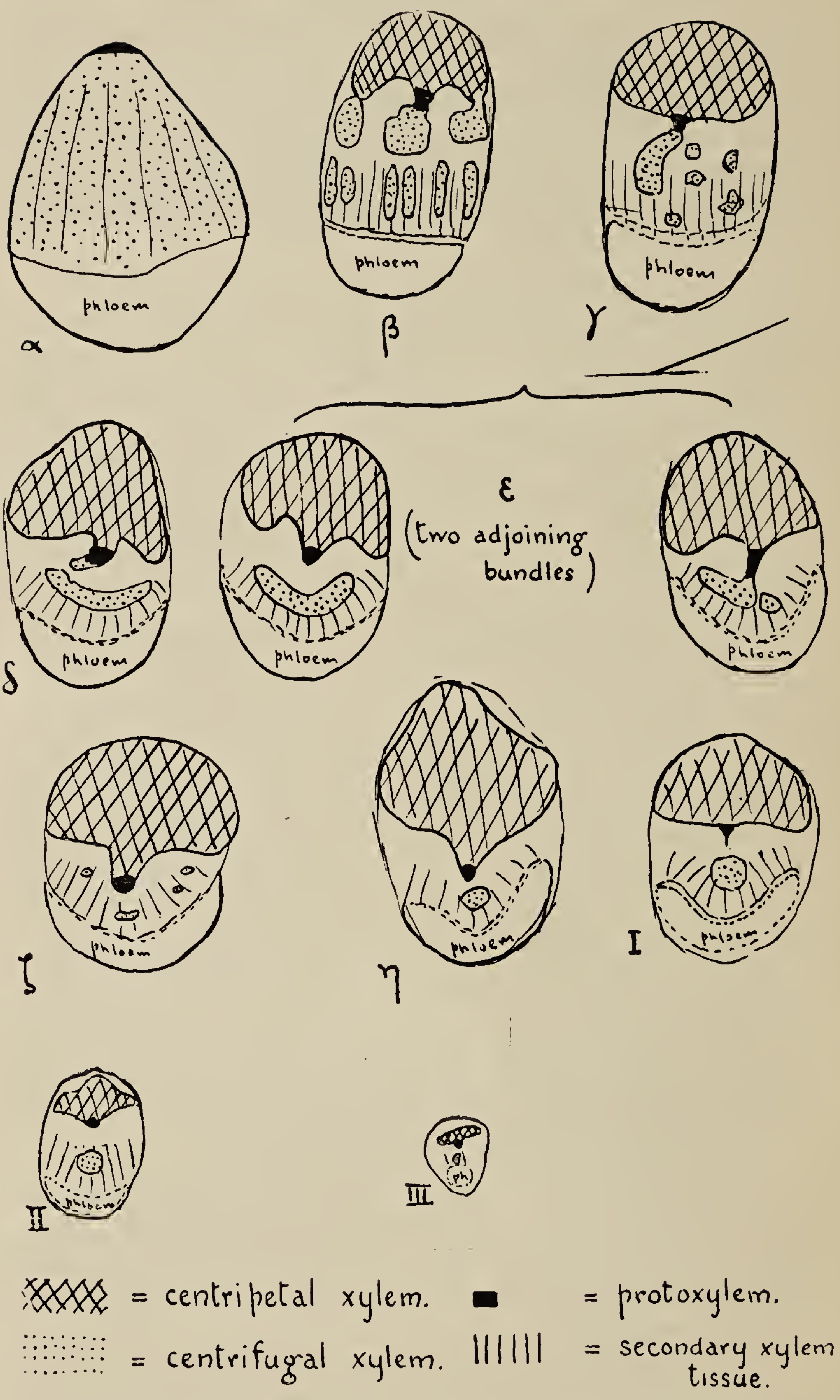


FIG. 5.—Petiolar Bundles. α—η, in acropetal order, from the basal centimetre of the petiole; I, from the petiole, between the base and the lowest pinnæ; II, from the midrib of the terminal leaflet ("*b*" of Fig. 6); III, from the tip of the terminal leaflet ("*a*" of Fig. 6).

It should be mentioned that mucilage canals are very abundant all through the plant. Some are large and lie free in the cortex, while other smaller ones run next the phloem in connection with the bundles, following them right into the laminæ, where the great amount of stain taken up by the mucilage often makes the structure of the small bundles difficult to ascertain.

THE LEAF.

The main features of the leaf are given by Kraus and Nestler and with their results my own observations generally agreed. The number of strands in various parts of the petiole and midrib is not such a definite thing as Nestler gives one to understand: in the leaves examined the numbers were seen to be less. My investigations were, however, mostly along a different line: they were directed chiefly to a study of the "mesarch" bundles of the leaf.

The petiole shows in transverse section a number of bundles distributed in relation to the two rows of pinnæ and forming the usual inverted *omega*. Pavolini records the occurence of "medullary strands" in the petiole, but there was none present in the material which I examined.

It is convenient to deal first with the connection between the endarch cortical leaf-trace and the "mesarch" petiolar bundle. It was found that the transition from one type to the other took place in the basal centimetre of the petiole and a series of seven sections across this basal centimetre was cut. They were cut at approximately equal intervals and called α—η in acropetal order. I have drawn typical bundles from each section by means of the camera lucida and these form the diagrams of Fig. 5. In α the structure was entirely endarch but in β there was a small group of centripetal elements. The centrifugal xylem here was much more loosely arranged than in α or in the cortical leaf-trace bundles. There is a fairly definite differentiation of the centrifugal xylem into an outer secondary portion in which the elements are arranged in rows and an inner primary portion whose tracheids are in less regular arrangement, and are connected with the centripetal elements. A cambium is present here as in all bundles of the petiole and midrib, at whatever level, cutting off, on the outside, phloem, and on the inside, centrifugal xylem, both tracheids and parenchyma. γ—η show a progressive increase in the size of the centripetal portion of the xylem and a decrease in the amount of the centrifugal wood. The centrifugal becomes more completely of the secondary type, *i.e.*, it appears in connection with the rows of cells cut off by the cambium. The portion which I have designated primary persists to different extents in different bundles. In some, even in sections ζ and η, there is a connecting band of tracheids between the two kinds of xylem, but in all cases this disappears sooner or later and at a level of about 2 cm. from the base leaves a group of bundles with centripetal and centrifugal xylems quite distinct from one another. It might be mentioned that the section depicted in Scott's "Studies in Fossil Botany" (2nd ed.), Fig. 133, is probably fairly near the base, as one of the products of the bifurcating bundle there shown has retained the connection between the two kinds of wood. The centrifugal wood does not consist of scattered elements, as in *Cycas*, but forms a compact mass in the median line of the bundle (see Figs. 8 and 9).

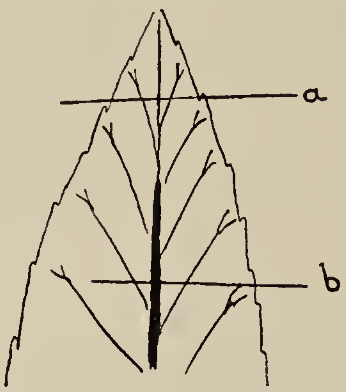


FIG. 6.—Tip of terminal leaflet to show position of sections "*a*" and "*b*" described in the text.

Before leaving the basal region of the petiole, one may mention that Le Goc reports in the Cycads which he investigated, the occurrence at the base of the petiole of various types of bundle, collateral and concentric. In *Stangeria* all bundles were strictly collateral: the only apparent exceptions were bundles undergoing division in which the centrifugal xylem split and the resultant portions came to lie at diametrically opposite sides of the bundle before the centripetal xylem mass bifurcated. We may represent this by $* \blacksquare *$ where the asterisks are centrifugal xylems, and the dark mass centripetal xylem. In all higher parts of the petiole bifurcation of a bundle takes place about a plane at right angles to this, which we may represent so :— $\overset{*\quad *}{\blacksquare}$ giving $\overset{*}{\blacksquare}\ \overset{*}{\blacksquare}$ Here we still see that the centrifugal is divided before the centripetal (see Fig. 8).

Turning again to our consideration of the changes in the bundle as we pass from the base upwards, we find that at the level of η we have very little centrifugal xylem. Usually there are only four or five lignified elements, but sometimes tracheids are entirely absent. As one passes up the petiole it is found that the amount of centrifugal xylem does not decrease, as has often been stated, but at a level just below the insertion of the first pinnæ there is, on the average, two or three times as much centrifugal wood as there is at a centimetre or two above the base. This large amount of centrifugal xylem persists up the rachis and into the midribs of the pinnæ. In the terminal leaflet, whose tip is represented in Fig. 6, two sections were cut, one above and one below the point at which the midrib suddenly and characteristically becomes very faint. In "*b*" the amount of centrifugal xylem, formed in connection with a well-marked cambium was very little less than that of the centripetal xylem (see Fig. 9), while even in "*a*" the midrib showed about five lignified centripetal elements and one well-marked centrifugal tracheid. Only in the lateral veins in "*a*" were all signs of centrifugal tracheids missing.

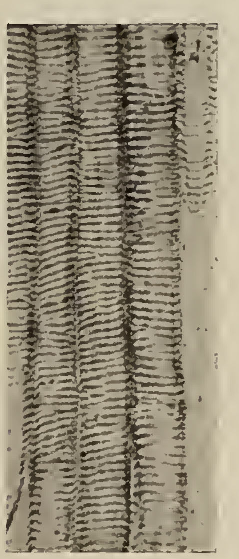


FIG. 7.—Longitudinal section of tracheids from wood of stem.

It is obvious from this that the centrifugal xylem system is not a thing (in *Stangeria* at any rate) that gradually dies out from the base to the tip of the leaf. Its amount increases over a large part of this length and it persists in the lamina almost as long as the centripetal portion.

Then we have its invariable formation in rows in association with a cambial layer, and in the light of Le Goc's proof that secondary growth occurs in Cycad leaves, we are almost certainly justified in calling the *Stangeria* centrifugal wood secondary. At the base we have a centrifugal xylem, not arranged in rows, which connects the two systems which are disunited in the higher regions of the leaf. This connecting portion is probably primary and thus connects up the Cycadean foliar bundle with the truly mesarch bundles of the Cycadofilicales. Even in the bundles of the main part of the petiole of *Stangeria* we have a vestige of this primary centrifugal wood in the median line of thickening which often stretches out from the protoxylem towards the centrifugal wood (Fig. 8).

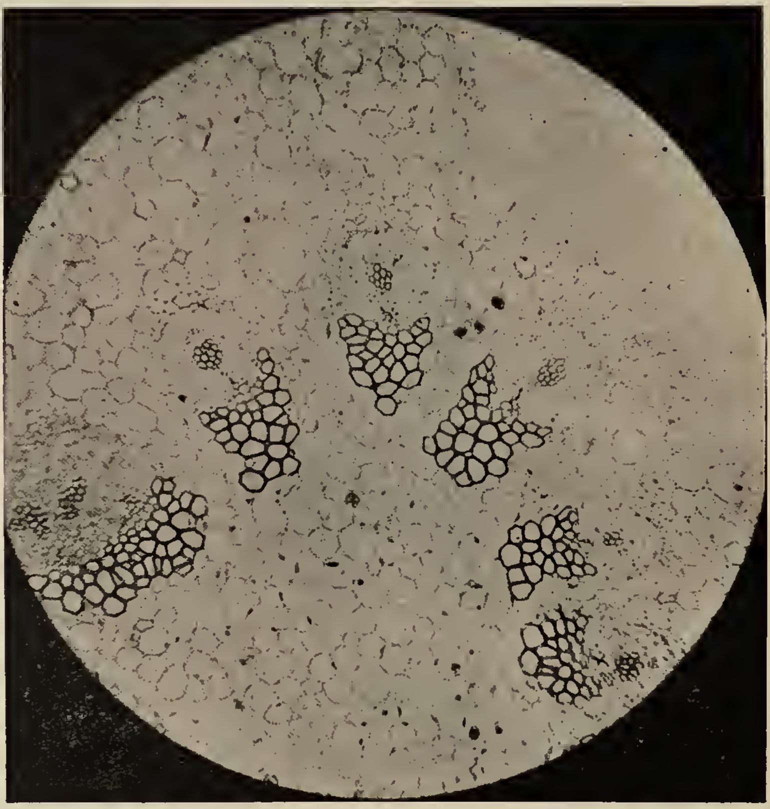


FIG. 8.—Transverse section of the petiole of *Stangeria*, between the leaf-base and the insertion of the lowest pinnæ.

STRUCTURE OF THE WOOD ELEMENTS OF THE PETIOLE.

Longitudinal sections were cut both near the base (but above the transition region) and at some distance up the petiole and in each case the structure of the elements was the same (Fig. 10). The centripetal wood showed a spiral protoxylem, while the metaxylem had pitting of a close scalariform type, quite in contrast with the annular-reticulate or open scalariform pitting of the centrifugal xylem, which resembles the wood of the stem.

Since in the stem of *Stangeria* there is so little distinction between primary and secondary wood one may be justified in assuming that the centrifugal elements of the petiole, even though entirely secondary, show the pitting actually and primitively characteristic of primary centrifugal wood. Granted this, we have a remarkable resemblance between *Stangeria* and those Cycadofilicales in which the mesarch bundles of the stem show centripetal xylem with a higher order of pitting than that of the centrifugal primary xylem. It is in connection with this point that Le Goc says "the difference in the nature of the xylem cells could also be quoted . . . . ; but this is of little value, as the nature of the centrifugal xylem varies so much and so rapidly with the distance from the protoxylem, giving in succession spirally thickened, annular, scalariform, pitted and multiseriate pitted tracheids."

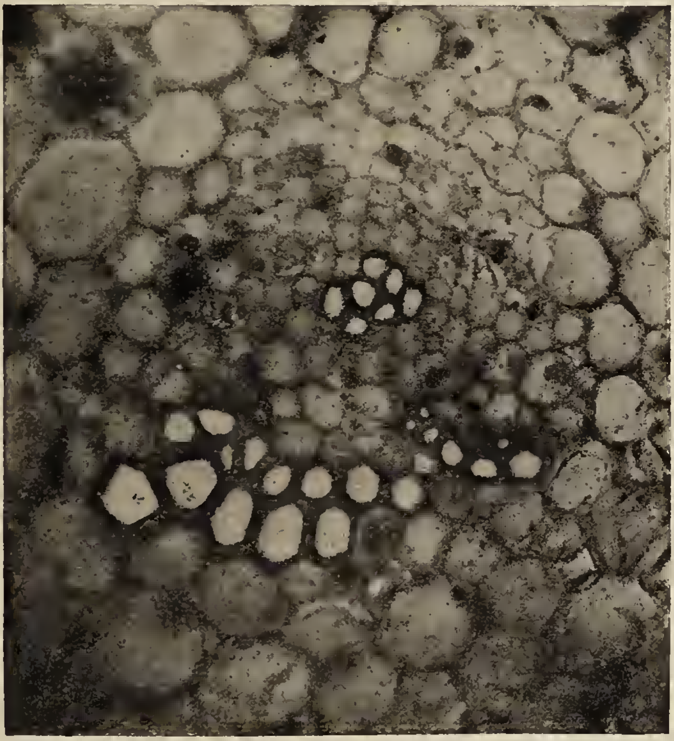


FIG. 9.—Transverse section of bundle from midrib of terminal leaflet at level "*b*" of Fig. 6.

In *Stangeria* this confusion of types of pitting is absent, but the clear parallelism is still left between its mesarch bundles and those of *Lyginopteris*, and from this case we can apply the results to the other Cycads in which the immediate assumption is, as Le Goc remarks, unjustifiable.

STEM WITH VASCULAR SUPPLY TO CONE.

In detailing the material used it was not mentioned that a large stem was treated with *Eau de Javelle* in the same way as that employed for the small stem. The results were nothing like as satisfactory, but the general arrangement of the bundles appeared to be the same as that described above. There were also present in one series of sections the bundles of a formerly produced cone. These were given off from points along one half of the vascular ring, and gathered together to form a fan-like mass which passed through a gap in the opposite half of the bundle-ring. This is exactly similar to that described for *Stangeria* by Solms Laubach (8).

CONCLUSION.

The principal theoretical conclusion arrived at from this work is that from the structure of the petiolar bundles of *Stangeria,* and presumably of other Cycads, a close relationship can be argued between the modern Cycadales and the fossil Cycadofilicales.

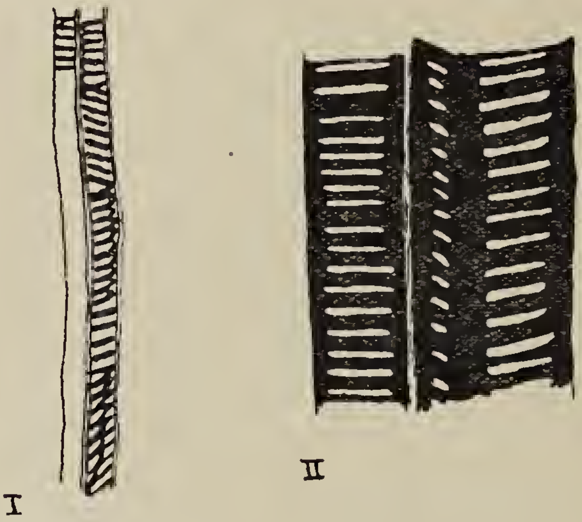


FIG. 10.—Longitudinal section of tracheids of petiole. I, centrifugal; II, centripetal.

The "mesarch" foliar bundles of one type are to be derived from a truly mesarch vascular strand with secondary centrifugal wood. Such a type is found in the stems of such forms as *Lyginopteris* and from this we evolve the modern structure by dropping out the lignification of the primary centrifugal xylem, leaving two distinct systems separated in space—the *centripetal* and the *secondary centrifugal.* The evidence for this is the successional series at the leaf-base (where, as Sinnott (7) has pointed out in his work on fern leaf-traces, primitive structures are known to persist) leading at a slightly higher level not only to normal forms, but also to bundles with no centrifugal lignified elements and to others with a persistent chain of elements joining centrifugal and centrifugal. This probably recapitulates a stage in evolution when both primary and secondary centrifugal wood were greatly but equally reduced, but at a still higher level in the petiole we have the secondary centrifugal reasserting itself and increasing in amount. As long as even a midrib persists we have the development of a cambium in relation to which the centrifugal xylem is formed, not as a dying-out vestigial structure, but with all the appearance of a definite functional tissue.

Further indication of the connection between these Cycad bundles and those of the *Lyginopteris* type is found in the parallel between the comparative histological characters of the centrifugal and centripetal tracheids.

SUMMARY OF RESULTS.

1. *Stangeria* possesses a stem with a feebly developed single ring of xylem, the groups of which are widely separated from one another.
2. The tracheids are, except for the protoxylem, thickened in a rather loose scalariform manner. Pitted tracheids are not found.
3. The vascular supply to each leaf generally consists of a typical girdle, plus four additional strands running directly from the central cylinder to the leaf-base.
4. The foliar bundles contain both centripetal xylem and centrifugal xylem, the two systems being separated in space. The latter is formed in radial rows in connection with a cambium and is probably all secondary. At the base of the petiole primary centrifugal wood connects centripetal and centrifugal secondary.
5. The centrifugal xylem is a flourishing tissue and not merely vestigial.
6. From the anatomy of the leaf-base and the characters of the pitting of the two kinds of wood it is concluded that there is close relationship between the foliar bundles of Cycads and the mesarch bundles of Cycadofilicales of the *Lyginopteris* type.

Finally I must express my thanks to Professor Seward, who has not only suggested the research and obtained the material for me, but has also given valuable help and advice at all stages of the investigation; to Mr. H. A. Hyde, who assisted me in preparing the stem for the examination of the girdle-system, and who took the photographs illustrating this article; and to M. M. J. Le Goc for the loan of the manuscript of his yet unpublished work,[1] which has done so much to clear up many doubtful points in Cycad anatomy.

---

[1] Published while the present paper was being printed (Annals of Botany, Vol. 28, 1914, pp. 183-193).

BOTANY SCHOOL,
CAMBRIDGE. *November 1913.*

LITERATURE REFERRED TO.

1. Coulter and Chamberlain. "Morphology of Gymnosperms." Chicago, 1910, and literature there cited.
2. Kraus. "Ueber den Bau der Cycadeenfiedern." Pringsheim's Jahrbücher IV, 1866.
3. Le Goc. "Observations on the Centripetal and Centrifugal Xylems in the Petioles of Cycads." Annals of Botany, XXVIII, 1914.
4. Nestler. "Ein Beitrag zur Anatomie der Cycadeenfiedern." Pringsheim's Jahrbücher XXVII, 1895.
5. Pavolini. "La *Stangeria paradoxa*, Th. Moore." Nuovo Giorn. Bot. Ital. XVI, 1909.
6. Scott. "Studies in Fossil Botany." London, 1909.
7. Sinnott. "Evolution of the Filicinean Leaf-Trace." Annals of Botany, XXV, 1911.
8. Solms Laubach. "Die Sprossfolge der *Stangeria* und der übrigen Cycadeen." Botan. Zeitung XLVIII, 1890.

INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION (I.P.E.) IN AMERICA, 1913.

(*continued from Vol. XII, p. 336*).

The Great Plains Region—Akron, Colorado.

AKRON is a little town, very typical of the newer "middle west," lying in the heart of the Great Plains about 100 miles from the eastern foothills of the Rocky Mountains. About four miles from the town is the experiment station of the United States Department of Agriculture—one of the most important of the federal agricultural experiment stations, and largely devoted to the interests of the dry-farming and stock-raising carried on in this district.

At this station members of the staff of the Bureau of Plant Industry of the federal department have for some years been carrying on a series of very important large scale experiments on the water requirements of plants—particularly of the commonly cultivated crop-plants—wheat, alfalfa, sorghum, corn, etc., and of the native plants also. An account of the first series of these experiments by Drs. Briggs and Shantz has just been published (Bulletin 284 of the Bureau of Plant Industry, 1913). In 1911

Dr. Shantz published a Bulletin in the same series (No. 201) entitled "Natural Vegetation as an Indicator of the Capabilities of Land for crop-production in the Great Plains area," and giving an excellent account of the natural vegetation of this neighbourhood and of its relation to the crops.

The international party arrived at Akron early on the morning of August 10th, and was joined by Professor and Mrs. Clements. Two days were spent in the neighbourhood. The members of the party not only had the opportunity of studying the native vegetation under the guidance of Mr. T. H. Kearney and Dr. Shantz, but were also able to inspect the experiments above mentioned under the guidance of Drs. Briggs and Shantz, and to obtain a first-hand idea of the methods of work. A particularly fine set of automatically recording instruments for measuring meteorological and other physical factors is installed at the station. Automobiles were most kindly lent by the principal citizens of Akron, and these made it possible to visit in a day the sand-hill region near Yuma, about thirty miles from Akron, as well as various typical associations of the Great Plains passed *en route*.

The Great Plains region covers an enormous area of country, extending northwards into Canada and southwards as far as Texas, with strikingly little change in the essential character of the country and of the vegetation. In physiographic character the Great Plains are very uniform, consisting of flat or gently rolling grassland on a clayey or loamy soil. Over considerable areas there are large deposits of sand, and these form sand-dunes in all stages of fixation by vegetation, and of rejuvenescence by the formation of blow-outs, and bear a distinctly different vegetation from the finer grained more compact soil of the rest of the area. The region is intersected by stream-courses, most of which are dry "sand-draws" for most of the year. Only the larger rivers, such as the Platte, the Republican and the Arkansas, rising in the Rocky Mountains or the foothills and running through to the Missouri-Mississippi system, maintain their streams at all times.

The main area of the plains is covered by the "short grass" association, dominated by the grama-grass (*Bouteloua oligostachya*) and the Buffalo-grass (*Bulbilis* or *Buchloë dactyloides*). Under the natural conditions these grasses do not attain a height of more than 2 or 3 inches above the soil. They form a fairly close sod with little bare soil showing between the plants. Associated are such plants as *Festuca octoflora*, *Plantago Purshii*, *Salsola pestifer*, *Munroa* *squarrosa* (annual), and *Schedonnardus paniculatus, Opuntia polyacanthya, O. fragilis, Mamillaria vivipara, Malvastum coccineum, Grindelia squarrosa, Ptiloria pauciflora, Gaura coccinea, Aragallus Lambertii*, etc. (perennial). In 1913 *Grindelia squarrosa* occurred in enormous quantity in the Akron district, its erect bright-green shoots, a foot or more high, forming a striking constrast to the grey of the short grasses. After rain the short grasses turn rapidly green—only to revert to the grey colour of their dry state in the succeeding drought.

The competition for water in the upper layers of the loamy soil is very severe. The short grasses by their shallow rooting habit are well adapted to utilise the rain directly it falls, and owing to this fact and to the intense evaporation and the slow percolation through the heavy fine-grained soil, very little water ever reaches lower levels. Soil boring clearly shows that while a certain amount of moisture is retained during drought in the surface-layers of soil, the underlying layers are extremely dry and the water they hold is unavailable to plants. The factor of the capillary rise of water does not enter into the conditions. Local irregularities in the compactness of the soil, however, cause considerable differences in the water-relation, and where the soil is looser percolation increases, deeper rooting plants flourish, and partly or completely exclude the short grasses. These water relations are no doubt the main explanation of the absence of trees in the Great Plains. When the soil is broken and trees are planted they make healthy growth though they do not attain any considerable size. It is certainly not true that the dryness of the air excludes tree-growth in this region. If the soil is broken by ploughing and left fallow the ground is first colonised by an open association of ruderals including *Amaranthus græcizans, Salsola pestifer, Festuca octoflora, Plantago Purshii, Munroa squarrosa, Chenopodium* spp., etc. This gradually gives place to an association in which the yellow flowered composite *Gutierrezia sarothræ* and the grey *Artemisia frigida* may share dominance. The former species is on the whole more southern and the latter more northern in distribution, but in the central region of the plains the two are generally associated, and in this association also occur *Bouteloua oligostachya, B. curtipendula, Mentzelia nuda, Petalostemum purpureum, Paronychia jamesii, Eriogonum effusum*, etc.

The *Artemisia-Gutierrezia* association gradually passes over, by the increasing dominance of the short grasses, into the typical climax or "chief" association of the formation. The whole succession from fallowing back to short-grass takes from twenty to fifty years to complete. Parallel with this succession following ploughing a natural succession may be traced where areas of disintegrating rock occur. Here a lichen association takes the place of the weed association of fallow arable, and gradually passes over into the *Artemisia-Gutierrezia* association, which in this case is richer in associated species. The remainder of the succession is essentially the same, though in some cases the *Artemisia-Gutierrezia* association may maintain itself against the short-grass invasion for a long time. Locally, particularly on "adobe" soils, the wheat-grass association, dominated by *Agropyrum Smithii*, occurs. This association is much more widespread further to the north, for instance in the Dakotas.

On the areas of sandy soil there is, as has been said, quite a distinct vegetation which is much more luxuriant than the short-grass vegetation. This is owing to the fact that the rain-water percolates through sand much more quickly, and the air-dry surface-layer acts as a dry mulch, checking evaporation from the deeper layers. The plants are deeper-rooting and have a larger available water-supply. The typical climax vegetation is dominated by the tall bunch grass (*Andropogon scoparius*)—a dry prairie-grass which has been already noticed as occurring on the Lake Michigan sand-dunes. Associated with the bunch-grass are such species as *Bouteloua hirsuta*, *Andropogon Hallii*, *Calamovilfa longifolia*, *Panicum virgatum*, *Psoralea tenuiflora*. *Eriogonum annuum* is scattered thickly through the association in places.

The sand-hill succession is started by a "blow-out" which provides an area of bare sand. This is colonised by *Muhlenbergia pungens*, *Redfieldia flexuosa*, *Psoralea lanceolata*, and *Petalostemum villosum*, forming an open association; and is followed by the sand-hills mixed association (Shantz), a very variable "intermediate" association characterised by a large number of species, including *Yucca glauca*, *Bouteloua curtipendula*, *Andropogon scoparius*, *Artemisia canadensis*, *Ipomœa leptophylla*, *Thelesperma gracile*, *Sorghastrum nutans*, *Chrysopsis villosa*, *Amorpha canescens*, etc.: and this in turn by the bunch grass association.

If the bunch grass association is broken by ploughing and left alone ruderals at first colonise the ground and are followed by the sand-hills mixed association: eventually the bunch grass returns. If on the other hand it is burned over or cut, and then grazed, the surface-layers of the soil being hardened, short-grasses come in, More or less intermediate between the two formations stands the wire-grass association dominated by *Aristida longiseta.* This occurs on Great Plains soils which are rather more sandy than those carrying the typical short grass association, but is included by Dr. Shantz in the short grass formation.

For a full and most interesting description of the vegetation whose characters have been briefly outlined, the reader should consult Dr. Shantz's bulletin already referred to.

The ordinary "dry farming" practice in this region is to fallow the land in alternate years. The surface-layer of dry soil acts as a dry mulch and preserves much of the water of precipitation falling during the fallow year in the deeper layers of soil. Thus a much better crop is obtained during the next year. The proceeding is however exceedingly risky, because a year of extreme drought may upset the calculation, and it is perhaps doubtful if even over a series of years, much advantage is obtained. "Dry farming" in this region scarcely pays except in association with ranching.

Of abundant ruderal weeds the so-called Russian thistle (*Salsola pestifer*) is the most conspicuous. This and some other species (e.g., *Amaranthus græcizans*) belong to the class of "tumble weeds," *i.e.*, they easily become uprooted or broken off and blow about the plains where they may often be seen caught in lines at the wire fences. *Salsola* shows very beautifully, when growing on the edge of a crop bordering on fallow, the marked effect of differences of water-content of the soil in determining root-growth. The roots of such a plant are all bent out, sometimes at right angles to the vertical axis, away from the crop and towards the fallow, and such plants are much larger and more luxuriant than those growing actually among the crop-plants. Similarly on the edge between a crop and an area of short grass, the Russian thistles have their roots bent *towards* the crop where the competition for water is less severe than in the short grass area. These phenomena give an excellent idea of the very severe competition for soil water that must go on in any closed association in this region.

Leaving Akron in the late afternoon of August 11th, the party travelled to Denver and thence southward to Palmer Lake on the edge of the Rocky Mountain foothills. Before reaching Denver an irrigated region is entered, a region in which a supply of river water is available for irrigation; and here the country is much more closely occupied by crops, and these are, on the whole, much more luxuriant than in the "dry farming" region further east. All along this part of the route the "sweet clover" (*Melilotus alba*) is exceedingly abundant and luxuriant as a roadside weed, far more so than in Europe, often forming pure stands for some distance along the wayside: indeed the abundance and luxuriance of this plant right through the continent from east to west, except in the driest and most alkaline regions, is a very striking phenomenon to a European. It seems that in temperate North America the plant has found much more favourable conditions than exist in Europe, its native home. *Typha latifolia* and *Scirpus validus* (?=*lacustris*) occur here and there in wet places, along the sides of the railroad tracks and elsewhere right through the prairie and plains regions, growing in places where no open water exists, rather a striking difference from their ordinary European habitats.

THE ROCKY MOUNTAIN FOOTHILLS.

August 12th was spent in an excursion from Palmer Lake into the "Black Forest," a great area of *Pinus scopulorum* (the Rocky Mountain form of the far western Yellow Pine, *P. ponderosa*), stretching out from the mountains on higher ground into the Great Plains, and with an average elevation of 1,000 feet above the latter. It occupies the watershed between the Platte river on the north and the Arkansas river on the south. The undergrowth of the pine forest consists largely of *Arctostaphylos Uva-ursi*, with *Muhlenbergia gracilis*, *Carex scoparia*, etc. The highest ridge of the forest has Douglas fir, representing the next higher stage in the Rocky Mountain zonation, but this ridge was not visited.

The pine forest is fringed with "chaparral" or, as we should call it, scrub,[1] dominated by the three species *Cercocarpus parvifolius*, *Quercus Gunnisonii* (a scrub oak), and *Rhus trilobata*, which are often mixed, but sometimes zoned. According to Professor Clements they have different water demands in an ascending series, and correspondingly the last-named species extends furthest eastwards. The chaparral often forms fairly dense thickets and casts a deep shade. It shelters various shade forms of species which also grow in the grassland outside, such as *Achillea lanulosa* (close to *A. millefolium*), *Helianthus rigidus*, *H. pumilus*, *Agrostis hiemalis*, as well as shade species—such as *Fragaria vesca*—which also occur in the Rocky Mountain forest.

The grassland which generally occupies the floors of the natural amphitheatres—the slopes of which are fringed with chaparral, the higher ground being covered with pine forest—is part of the

---

[1] To be distinguished from the "true" Californian chaparral which is sclerophyll scrub quite analogous to Mediterranean *maquis*

Great Plains grassland formation, but is not here dominated by short-grass, and consists largely of *Festuca ovina* (forma *ingrata*) *Bouteloua hirsuta*, and *Kœleria cristata*, with *Achillea lanulosa*, *Petalostemum* sp. *Artemisia canadensis* and *Arenaria Fendleri*, abundant. This grassland also covers the strikingly flat tops of the foothill "mesas"—the dissected remains of an old alluvial plain—and here is often dominated by the grama-grass, *Bouteloua oligostachya*, with *Muhlenbergia punctata* and *Agropyrum Smithii* forming nearly pure local patches (societies in the English use) and much *Opuntia* and *Mamillaria vivipara*, giving quite a typical Great Plains vegetation.

On the evening of August 12th the party travelled—again southward—to the flourishing city and health resort of Colorado Springs, where the night was spent. On August 13th the party drove west to Colorado City, spending the day among the foothills, and examined the vegetation of Bear Canyon, of the Niobrara Limestone, which here forms a prominent foothill ridge, and of the "Garden of the Gods" with its towering masses of red Triassic or Permian sandstone. In this region the foothill thicket (chaparral) alternates with grassland and on the rocky slopes the most northern limit of the Pignon-Juniper formation is encountered. This last formation, dominated by *Pinus edulis* and *Juniperus monosperma* (*Sabina scopulorum*), has an immense extension to the southward through New Mexico and Arizona into Mexico. At this northward limit its specific flora is relatively poor, being mainly characterised by *Stipa Scribneri* with the fern *Cheilanthes Feei* on the rocks. It takes the rocky slopes with shallow soil, while the chaparral prefers the gentler slopes with a deeper soil. Examples of river bottom woods dominated by *Populus Sargenti* (the western form of the cottonwood) and with *P. augustifolia*, *Acer Negundo*, etc. associated, sheltering quite a characteristic river-bottom vegetation, were seen in Bear Creek Canyon. In the evening the party walked from Manitou (6,500 feet) at the foot of the mountains up Engelmann Canyon which carries the Pike's Peak cog-railway, to Minnehaha-on-Ruxton (8,330 feet) a beautiful spot in the Douglas fir-wood which covers the lower slopes of the Rocky Mountains, and here they were accommodated in Professor Clements's two bungalows and in the inn.

ROCKY MOUNTAINS—PIKE'S PEAK REGION.

The next week was spent at Minnehaha as headquarters, and almost daily excursions were made to places in the neighbourhood, including one to the top of Pike's Peak (14,109 feet) and another (2 days) to the top of Mount Garfield (12,365 feet). The opportunity thus afforded of studying the vegetation of this region in a more or less leisurely way, and the restfulness of the comparatively prolonged sojourn in so delightful a spot as Minnehaha, right in the midst of practically untouched forest and with a glorious view down the canyon over the Great Plains, were much appreciated by the party, who owe a special debt of gratitude to Professor and Mrs. Clements for their unwearying kindness and the great trouble taken to secure the comfort and convenience of all the members. During the stay at Minnehaha, Professor Engler of Berlin joined the party.

The Rocky Mountains in the Pike's Peak region are formed of Archæan granite weathering very easily into rough rounded fragments, largely ranging from 10 to 15 or 20 millimeters in diameter. This coarse gravel forms the very characteristic gravel slides which occupy many of the mountain slopes, and furnish the basis of the soil on which the succession to forest is developed.

Minnehaha is situated in the Douglas fir (*Pseudotsuga-mucronata*) zone, and all stages of the succession from bare gravel-slide to Douglas forest may be studied in the immediate neighbourhood. These stages may be summarised as follows, according to Professor Clements: (1) Gravel-slide association with *Aletes acaulis*, *Eriogonum flavum*, *Mentzelia multiflora*, *Smilacina* (*Vagnera*) *stellata*, etc., forming an open (pioneer) association with large areas of bare gravel between the plants. This association begins to colonise the gravel-slide directly the downward movement of the slide is checked from any cause. The plants all have extensively developed underground parts which ramify in the gravel and by upward growth of the shoot-buds are able to keep pace with the movement of gravel from above which tends to cover them. (2) Half-gravel slide-association with *Elymus triticoides* (*ambiguus*) and *Muhlenbergia gracilis* largely covering the ground. *Rubus deliciosus*, *Gilia aggregata*, *Geranium cæspitosum* and in places *Yucca glauca* are conspicuous species in this association. The half-gravel slide may be followed by (3) the thicket association, which may be regarded as the upward continuation of the chaparral which fringes the Great Plains. Indeed *Quercus Gunnisonii* is still found at this level, but dies out immediately above, and the thicket formation is here mainly composed of *Holodiscus dumosus*, *Rubus deliciosus*, and *Opulaster opulifolia* (*monogyna*), with *Jamesia americana* in company with the two last species extending to much higher altitudes. (4) The Pine forest association, dominated by *Pinus scopulorum* and in places by *P. flexilis.* The pine forest has an undergrowth, more or less discontinuous, especially of *Arctostaphylos Uva-ursi*, with *Pentstemon* spp., *Drymocallis* (*Potentilla*) *fissa*, etc., and the frequent tall grey-white spikes of *Frasera speciosa.* (5) The Douglas fir-wood association dominated by *Pseudotsuga mucronata* freely mixed with Engelmann spruce (*Picea Engelmanni*). The latter tree is dominant and forms forest at higher levels up to 11,000 feet. Both shelter a fairly rich ground-vegetation essentially similar throughout. When growing in very close stand rejuvenation in both forests ceases and the ground becomes almost bare of vegetation. The shrub-layer normally consists of *Acer glabrum, Betula fontinalis, Opulaster opulifolia, Holodiscus dumosus ;* and local dominants of the ground-vegetation are *Thalictrum sparsiflorum, Erigeron macranthus, Solidago Parryi, Mertensia pratensis, Fragaria vesca.*

After a burn of the mature forest aspen (*Populus tremuloides*) wood normally appears and is eventually replaced by Douglas fir. There is, however, another aspen association—the aspen-meadow, developed in the broader valleys at higher altitudes. The meadow-vegetation is much the same in the open as under the light shade of the aspens. Towards the wetter ground on the edges of the streams this is replaced by a birch-willow thicket. *Potentilla* (*Dasyphora*) *fruticosa* is a very conspicuous plant of such habitats.

The stages of the main (gravel slide—Douglas forest) succession alternate very strikingly on the slopes of the valleys about Minnehaha. Generally speaking the south and west-facing slopes are in earlier stages of the succession than those facing north and east.

In extreme cases a bare gravel-slide may face a Douglas wood on the opposite side of the valley. This, according to Professor Clements, is because of the prevalent west winds which help fires and keep the soil disturbed. On the south-facing slopes also the conditions are evidently drier and the succession less rapid. On the south-facing slope of Ruxton glen indeed there is a complex mixture of different stages of the sucession, and a great deal of telescoping often occurs, while many species come in out of their places, *e.g.*, Pine and Douglas fir sometimes directly follow on gravel-slide. A certain amount of scepticism was indeed expressed by some members of the party as to the generality of the succession outlined above, the view being taken that the different associations were likely to be stable under the conditions to which they were exposed. The present writer, while accepting the succession given above as normal, with much disturbance and telescoping owing to various causes, was inclined to doubt whether the pine forest, a very distinct association, occurring specially on wind-swept gentle slopes or on the broad, rounded tops of minor summits, would not in such situations tend to maintain itself indefinitely. Professor Clements's forthcoming book on the vegetation of this region will no doubt clear up many such questions. What seems to be wanted is a very clear statement, analysis and criticism of the evidence for the continuity of the sucession, of the conditions determining the initiation of each stage in the habitat presented by the preceding stage, and of the conditions under which disturbance and telescoping occur.

Space does not permit of an extended account of the vegetation of the upper ranges of the mountains, of which indeed, partly owing to bad weather, we did not see as much as could have been wished.

Above about 9,000 feet Douglas fir forest gives way to forest of Englemann spruce, which has much the same ground vegetation. Professor Schröter noted the following marked differences between the forest of *Picea Engelmanni* and the corresponding Swiss forest of *Picea excelsa*: absence in the former of plants germinating on fallen rotting trunks or on stumps; less humus and no specialised humus-plants; no *Usnea* on the trees. These negative features are no doubt to be attributed to the much drier air. *Picea Engelmanni* sometimes itself forms the upper forest-limit at 11,000 feet, but often gives way to *Pinus aristata*, which in that case forms the actual "timber line" and often presents fairly characteristic "Krüppelholz" forms. Above this there is no alpine scrub-association but we pass at once to alpine-meadow alternating with gravel-slides inhabited by quite a different set of species from those of lower levels. Cushion plants such as *Parouychia pulvinata*, *Arenaria biflora* and *Silene acaulis*, together with such forms as *Haplopappus pygmæus*, *Senecio taraxacoides* and *Festuca brachyphylla* are the characteristic species. The rock-cleft vegetation contains *Polemonium speciosum*, *Primula Parryi*, *Mertensia alpina*, *Claytonia megarrhiza*, etc.

The alpine meadow consists primarily of *Carex rupestris*, *C. filifolia*, *Festuca brachyphylla* and *Poa* spp., with societies of *Rydbergia grandiflora*, *Polygonum bistortoides*, *Mertensia alpina*, *Castelleia pallida*; and this is the main climax association above 11,000 feet.

According to Professor Clements it is preceded in succession on the one hand by alpine gravel-slide, on the other by alpine bog. The top of Pike's Peak itself is covered with "mountain-top detritus," holding a very scanty vegetation. The snow-line is of course well above the summit in this latitude with so low a precipitation—about 28 inches on the summit. There are two or three tiny glaciers in the neighbourhood of Long's Peak, 100 miles to the north.

A feature of the stay at Minnehaha was discussion on vegetation concepts: in particular a discussion in which the divergent views of the plant-formation were made very clear. Of the two main conceptions, one started with the formation as a purely local phenomenon, with a specific floristic composition, recognising analogies between any given formation and others with similar growth-forms in other parts of the world; the other considered a formation as a universal phenomenon with the same fundamental relations to environment wherever it occurs and represented in different places by communities of different floristic composition. To the acceptance of such a concept the adherents of the former view objected that we have not as yet enough accurate comparative knowledge of analogous plant-communities in different parts of the world to predicate identity of environmental relations, in spite of similarity or identity of growth-form. It is safe—and very satisfactory—to say that the phytogeographers present were all in substantial agreement as to what they meant by a plant-association, and this at any rate is a very distinct first step to that general agreement as to vegetation concepts which must eventually come.

On August 21st the party left their pleasant abode at Minnehaha and returned to Colorado Springs, where the members were most charmingly entertained to supper at the El Paso Club by some of the leading inhabitants of the city, where there is a large Anglo-American colony.

On the following morning, August 22nd, the party left Colorado Springs for Salt Lake City by the Denver and Rio Grande railroad. The route at first lay southward, skirting the foothills, and traversing the formations previously seen. *Atriplex canescens* and *Opuntia arborescens* are however conspicuous here in the Plains formation, and the sage-brush (*Artemisia tridentata*) begins to appear from the south. At Pueblo the line turns west and beyond Canyon City enters the Royal Gorge of the Arkansas river, bounded in places by abrupt cliffs 2,000 feet high. The Pignon-Juniper association is very well developed on the north exposure, with *Opuntia arborescens* largely represented on the south-facing side of the gorge. Further up the gorge this gives place also to the Pignon-Juniper association and then to Pignon alone. *Populus tremuloides* is abundant along the riverside. Further up still the gorge opens out and Douglas fir, Engelmann spruce and aspen appear on the upper slopes of the valley. Eventually a broad valley is entered, sub-alpine meadow containing much *Potentilla fruticosa* with *Picea Engelmanni* and *Pinus Murrayana* (the lodge-pole pine) which is absent from the Pike's Peak region, though it forms a well-marked altitudinal zone further north. Tennessee Pass, crossing the Continental divide at 10,246 feet, was reached about dusk and here are close stands of lodge-pole pine—perhaps fire relicts—among great stretches of bare grass-covered mountain.

(*to be continued*).

PTERIDOSPERM ANATOMY AND ITS RELATION TO THAT OF THE CYCADS.

By N. Bancroft.

[With Twenty Figures in the Text.]

THE question of the origin of the Cycadophyta is one of great interest, and regarded merely from an anatomical standpoint, it has provided ample material for discussion.

There are two main views concerning the origin of Cycadean vascular anatomy—first, that advanced by Scott (14, pp. 648-650) deriving it from the type possessed by Pteridosperms of the Lyginopteridean alliance; and secondly, that deriving it from the type exhibited by the Medullosean alliance, this latter thesis being upheld principally by Worsdell (23). There is much evidence in favour of both views, but this is only to be expected since the Lyginopteridean and Medullosean types of anatomy may be shown to be closely related through the simplest forms of each, the discovery of *Sutcliffia* (13) having been of great significance in this connection. Dr. de Fraine's recent description of *Sutcliffia* (3) is concluded by a third hypothesis with regard to the origin of Cycadean anatomy; this may be considered as a modification of

Worsdell's view, bringing it more closely into contact with that of Scott. A comparative consideration of the three opinions suggests that the three alliances—Lyginopteridean, Medullosean and Cycadean—are closely related so far as their anatomy is concerned, and this idea is fully confirmed by an investigation of reproductive and foliar organs in the three groups.

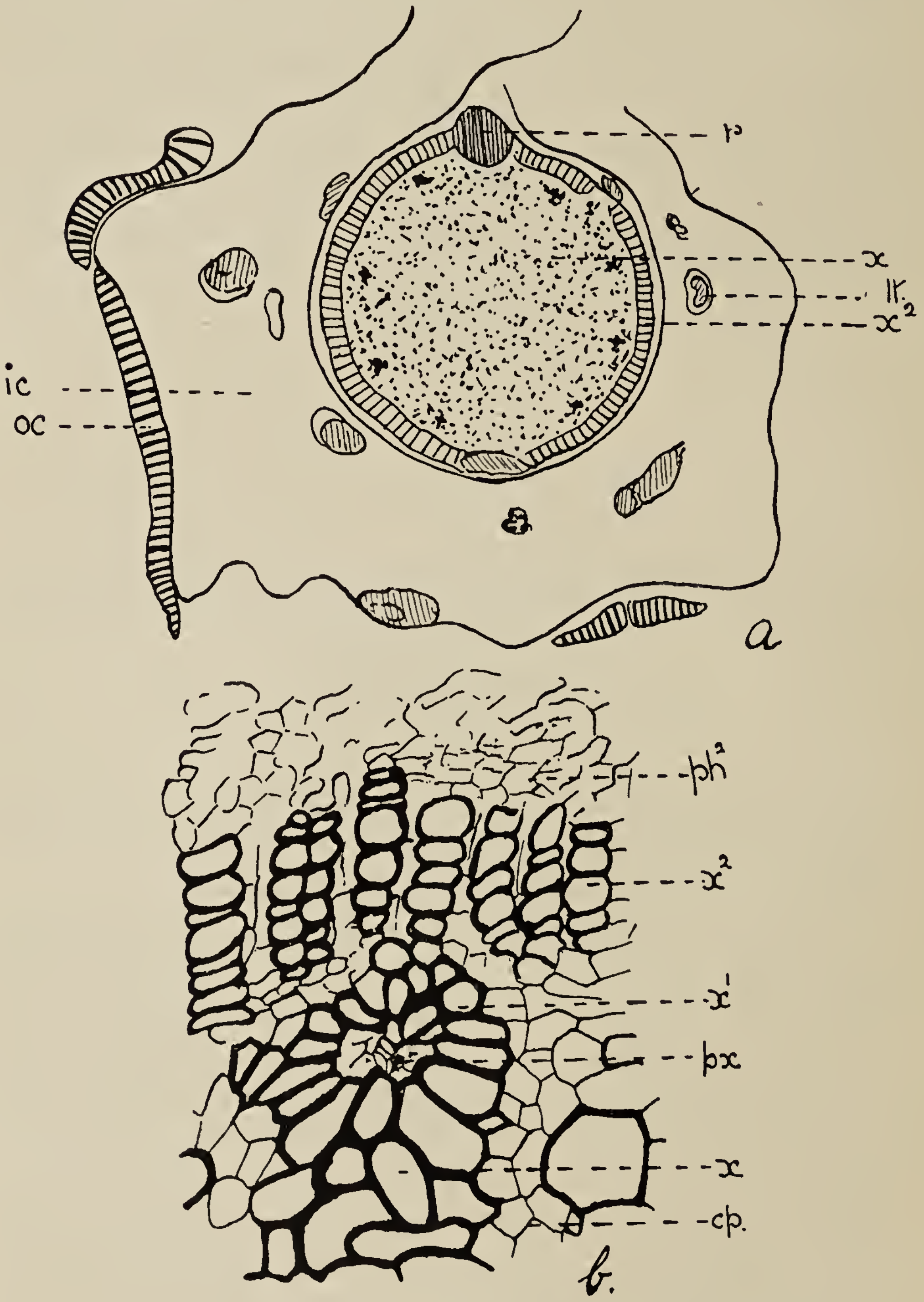


FIG. 1.—*Heterangium Grievii.* A, transverse section of stem. *x*, central mass of tracheides and parenchyma; x^2, secondary wood; *ic*, inner cortex; *oc*, outer cortex; *lt*, leaf-traces; *r*, base of a root. (Adapted from Scott, "Studies.") B, part of transverse section from outer region of stele, showing a primary xylem strand and adjacent tissues. *cp*, conjunctive parenchyma. (After Williamson and Scott, 1895).

Considering first Scott's theory with regard to the derivation of Cycadean anatomy from the Lyginopteridean type :—

Heterangium (19; 14, p. 401) is the simplest known member of this alliance. It is a genus having a considerable geological range, from the Scottish Calciferous Sandstone at the base of the Carboniferous, through the Coal Measures to the Permian beds of France. *Heterangium Grievii*, the oldest and best known species may be taken as typical of the genus. The specimens come from the Calciferous Sandstone of Pettycur, and the reference to the Lyginopterideæ is based mainly on vegetative characters, although it is supported by the association of the stems with seeds (*Conostoma*) of the same type as those of *Lyginopteris* (8, p. 111.)

The stem (Fig. 1, *a*) has a single vascular cylinder, that is, it is monostelic. The stele is solid, consisting of a central mass of grouped tracheides (the primary wood) and strands of conjunctive parenchyma; the tracheides are, as a rule, much more abundant than the parenchyma, and there is never any attempt, on the part of the cellular tissue, to form a pith. Definite clusters of tracheides are arranged peripherally and contain the spirally-thickened mesarch protoxylem elements, with which are associated a few parenchymatous cells (Fig. 1, *b*). These clusters of tracheides are continuous with the leaf-trace bundles. The primary xylem elements, apart from the protoxylem, typically possess multiseriate bordered pits on all walls. Most specimens show a development of secondary wood, the secondary tracheides bearing numerous bordered pits on their radial walls only. A ring of phloem surrounds the xylem and is succeeded by pericycle.

The leaf-trace bundles are of large size, and are usually without any secondary tissues. They are at first collateral, but become concentric before entering the leaf-bases. The traces in *Heterangium Grievii* usually remain undivided throughout their course, each petiole being traversed by a single vascular bundle of concentric mesarch structure. Other Heterangiums have double leaf-traces, this being the case in *Heterangium tiliæoides*, but here it appears that the two bundles unite in the petiole (19, p. 763).

The anatomy of *Heterangium* does not of itself indicate a connection with that of the Cycads. It is in the next type, clearly derivable from *Heterangium*, that the similarity between the recent and fossil types is seen.

Lyginopteris[1] (19; 14, p. 357) represents the next known stage in vascular evolution within the Lyginopterideæ. *Lyginopteris oldhamia* (Fig. 2) from the English Coal Measures, possesses a stem which is in all cases, according to Scott, of monostelic structure. But here the centre of the stele is occupied by a large pith instead of by tracheides and conjunctive parenchyma as in *Heterangium*. The pith is surrounded by from five to eight or nine distinct strands of elements mostly possessing multiserate bordered pits; these strands constitute the primary xylem of the stele. According to Scott, they are mesarch in structure, like the peripheral strands associated with protoxylem in *Heterangium* and are thus comparable with the petiolar bundles of Cycads.[1] There is more centripetal xylem than centrifugal, and a few parenchymatous elements accompany the protoxylem on the inner side. Immediately outside the ring of primary xylem strands, there is in all except the youngest stems, a broad continuous zone of secondary wood consisting of radial series of tracheides and medullary rays. The rays are sufficiently developed to indicate that the wood was originally of a somewhat parenchymatous nature, similar to that of recent Cycad woods. In well-preserved specimens, cambium and primary and secondary phloem may be seen.

---

[1] Potonié's name *Lyginopteris* is adopted here, as it is undoubtedly more correct than *Lyginodendron*, a name which has been used for quite different types. See Potonié, Lehrbuch der Pflanzenpalæontologie, p. 171, 1899.

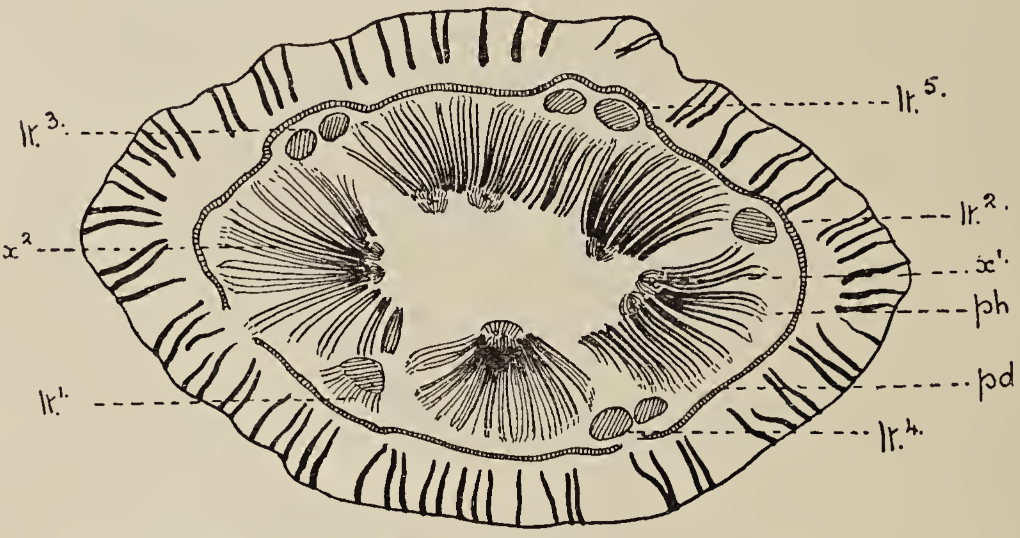


Fig. 2.—*Lyginopteris oldhamia.* Transverse section of stem. Surrounding the pith are eight primary xylem-strands; beyond these is a wide zone of secondary wood, and then the phloem. *ph*, phloem; *pd*, periderm, marking the outer limit of the pericycle; *lt*¹ to *lt*⁵, the five leaf-traces. (Adapted from Williamson and Scott, 1895).

The vascular strands surrounding the pith form the leaf-traces, which follow a nearly vertical course until they are free from the pericycle, when each trace divides into two and bends out sharply through the cortex to enter the leaf-bases. On leaving the stele, the leaf-traces have secondary wood which is generally lost by the time they divide. This constitutes an unimportant difference from *Heterangium*. As in that genus, however, the bundles remain collateral until they enter the petioles, having the appearance, according to Scott, of some of the partly-fused petiolar bundles of Cycads (14, pp. 364-365; Figs. 132, 133). In the petioles they become concentric in all cases, whether the twin bundles of the traces fuse again or remain separate (Fig. 3).

---

[1] Cf. the view of Chodat, quoted below, p. 49.

From the foregoing descriptions, it will be seen how similar *Lyginopteris* is to *Heterangium*—the mesarch nature of the primary xylem strands; the essential characters of the mesarch leaf-traces and petiolar strands; and the general histology of both types, indicate a close relationship between them. The chief anatomical difference lies in the fact that *Lyginopteris* possesses a pith, while the centre of the stele in *Heterangium* consists of tracheides and conjunctive parenchyma. According to Scott, *Lyginopteris* is "a *Heterangium* which has acquired a pith," (14, p. 646) owing to the progressive tendency to restrict water-conduction to the new or centrifugal wood, thus rendering development of the old primary centripetal wood unnecessary (cf. 12).

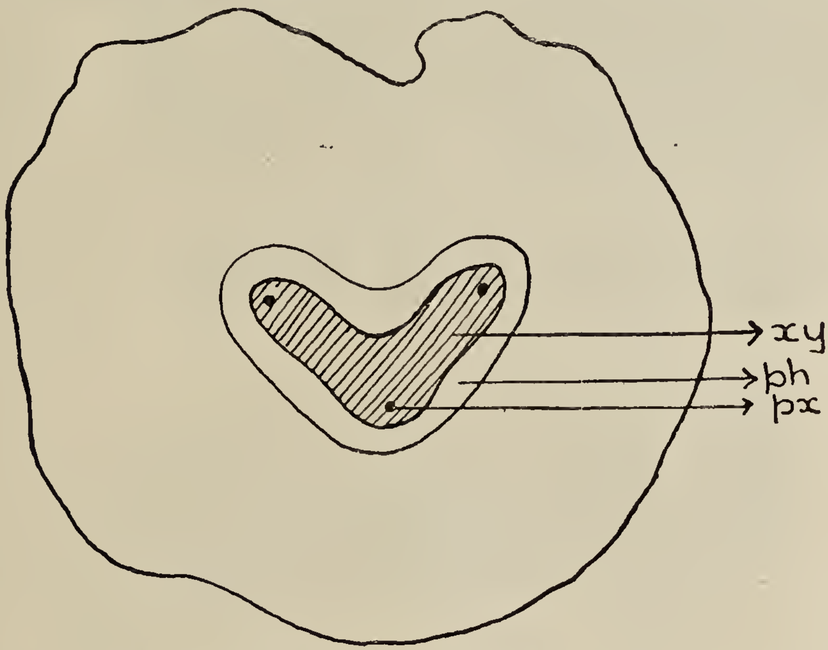


FIG. 3.—*Lyginopteris oldhamia*. Transverse section of rachis. *xy*, V-shaped xylem; *ph*, phloem completely surrounding xylem; *px*, protoxylem. (Adapted from Williamson and Scott, 1895).

Occasionally specimens of *Lyginopteris* have been observed to exhibit anomalies in anatomical structure; from the present point of view, the most interesting variation consists in the formation of secondary vascular tissues with inverted orientation, in the pith immediately within the normal ring. Sometimes the anomalous cambium is continuous through the leaf-gaps with the normal zone, so that each segment of wood is surrounded by a cambium and the stem has a polystelic appearance. This anomaly is particularly interesting in connecting the Lyginopterideæ with another group of the Lyginopteridean alliance—the Cycadoxyleæ. The secondary wood of the representative type—*Cycadoxylon robustum* (15)—resembles that of *Lyginopteris oldhamia* (Fig. 4). The medullary rays are broad and high, and must originally have imparted to the wood a very soft parenchymatous texture, like that, as Scott remarks, of a recent Cycad (14, p. 483). The tracheides bear multiseriate pits on their radial walls only. Strands of primary wood surrounding the pith—so characteristic a feature in *Lyginopteris*—have not been detected with certainty in *Cycadoxylon;* if present at all, they must have been much reduced, presenting an approach to the endarch condition of the wood of recent Cycad stems. Somewhat fragmentary leaf-traces are seen, here and there, passing out through the secondary wood; but in these again, the primary xylem is not evident. It cannot therefore be definitely decided whether the primary structure of the wood was of the *Lyginopteris* type, or whether the vascular structures were truly endarch as in the stem of recent Cycads. The stem presents a

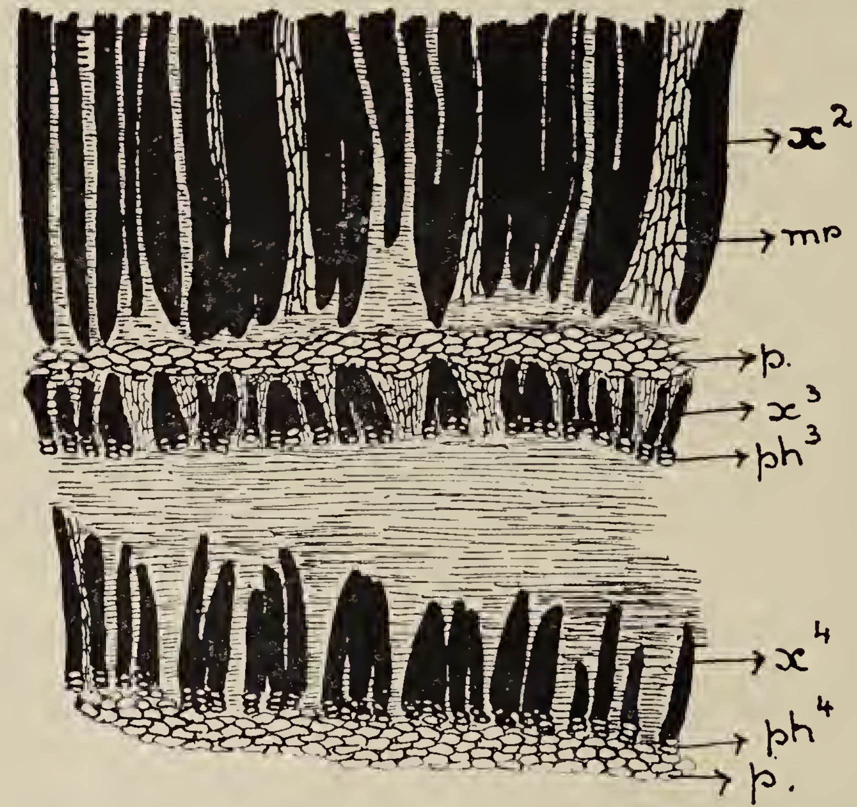


FIG. 4.—*Cycadoxylon robustum.* Part of transverse section of stem, showing inner portion of normal wood. x^2, with two inverted zones of wood and bast, x^3, ph^3 and x^4, ph^4; p, parenchyma; mr, medullary ray. (Adapted from Scott, "Studies.")

peculiarity of structure foreshadowed in some specimens of *Lyginopteris oldhamia*—the formation of one or even two inverted zones of wood and bast at the margin of the pith; and it is in this fact, coupled with that of the Cycadean nature of the secondary wood, that the interest of the fossil, from the present point of view, lies.

Cycadoxylon Fremyi (10; 14, p. 486) shows the same type of structure as *Cycadoxylon robustum*. There are two or more interrupted inverted zones of xylem and phloem, separated from the normal zone by parenchyma. Although there is still, according to Seward (15, p. 79), a trace of the mesarch structure of the xylem strands in the stem, it is clearly much reduced, so that the wood is very Cycad-like.

Ptychoxylon Levyi (Fig. 5) is another type of the Cycadoxyleæ in which extra zones of vascular structures occur (10; 14, p. 487). An outer more or less continuous cylinder of wood and bast surrounds the large pith, which contains several secondary vascular bands. Leaf- and branch-traces break the continuity of the central

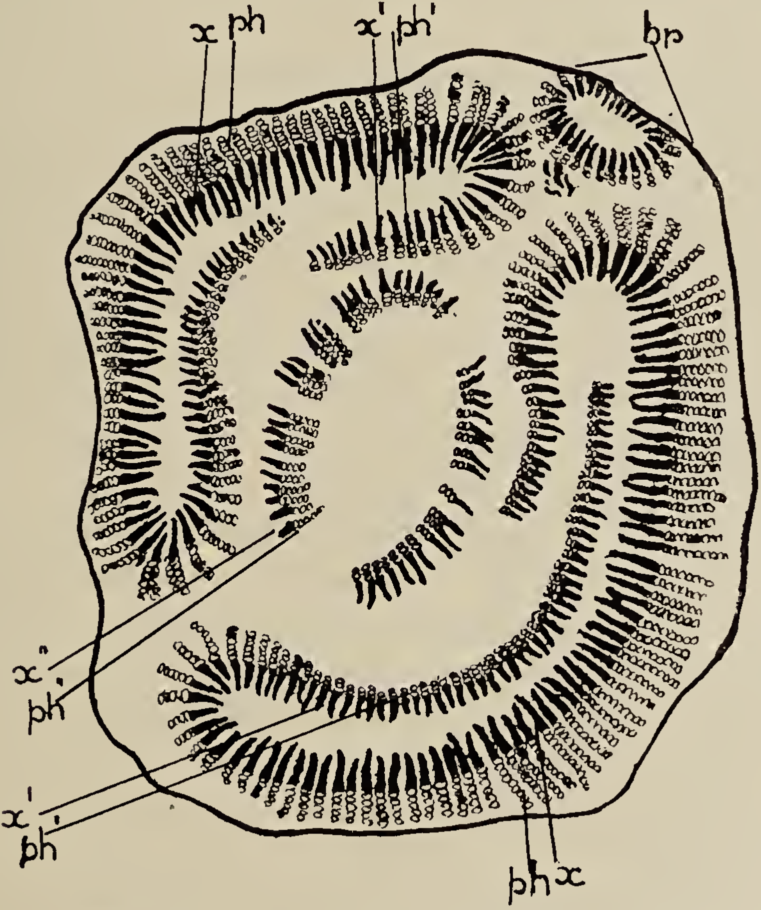


FIG. 5.—*Ptychoxylon Levyi*. Transverse section of a decorticated stem. *x*, *ph*, normal xylem and phloem; *x'*, *ph'*, first inverted medullary bands of xylem and phloem, continuous at the leaf-gaps with normal zone; *x''*, *ph''*, second inverted zone; *br*, stele of a branch. (Adapted from Renault, 1896).

cylinder, the edges of which become incurved to unite with two of the internal vascular bands; a connection between these and the normal vascular ring is thus maintained. A similar behaviour, it will be remembered, was noted in some specimens of *Lyginopteris oldhamia*, the anomalous vascular bands in this type being connected at the leaf-trace gaps with the normal vascular structures. The conditions in *Ptychoxylon* are more complicated however, for there are often two or three concentric systems of internal xylem and phloem, joining the external cylinder at different levels. Centripetal primary wood seems to be absent in the stem of *Ptychoxylon*, though the leaf-traces appear to have the same structure as those of *Lyginopteris*.

Dr. Scott, in agreement with Prof. Seward's views (14, p. 490; cf. 15), suggests that the Cycadoxyleæ "may have been derived from some form resembling *Lyginodendron oldhamium* from which they have deviated in two principal respects." Firstly, they have gradually lost the primary centripetal wood of the stem bundles, though apparently retaining it in their leaves. "This change is in a Cycadean direction, for the recent Cycads (as well as the Mesozoic Bennettiteæ) have wholly lost the centripetal primary wood in their vegetative stems, while retaining it in their leaves and occasionally in the peduncles of their cones" (14, p. 491). Secondly, the Cycadoxyleæ became modified by the formation of inverted medullary wood and bast, a constant and marked feature, foreshadowed as an individual and unimportant peculiarity in *Lyginopteris*. In this also there is a certain likeness to some genera of Cycadaceæ, for these are characterised by the formation either throughout the stem or locally, of extra wood and phloem, though in the Cycads these anomalous vascular structures are cortical and not medullary, as in the Cycadoxyleæ.

Reviewing the main points of Cycadean anatomy—(1) the retention of mesarch structure in petioles and peduncles of cones; (2) the parenchymatous nature of the wood; (3) the multiseriate pitting of the tracheides; (4) in *Bowenia*, *Cycas*, *Encephalartos* and *Macrozamia*, accessory zones or groups of xylem and phloem in the vegetative stem, with the joining of cambiums through leaf-gaps and the consequent formation of concentric bundles—it is seen that all these features are foreshadowed amongst fossils of the Lyginopteridean alliance; so that there is much support for Scott's view that the Cycads sprang from such a type as *Lyginopteris* itself. The Cycadoxyleæ cannot be considered on the main line of Cycadean descent, but *Lyginopteris* may represent a stock from which the Cycadoxyleæ arose as a side line, while the Cycads formed a more successful line of descent from the same stock. The so-called vascular anomalies appearing in some of the Cycad genera may be the expression of potentialities of development inherited from the ancestral stock, these potentialities manifesting themselves constantly in the other group, the Cycadoxyleæ. The parenchymatous nature of the secondary wood, the gradual disappearance of the centripetal wood of the stem, and its retention in the leaves, characterise both lines.

Prof. Weiss, in his Presidential Address to Section K at the British Association Meeting of 1911 (18, p. 5), draws attention to Chodat's criticism of the view that the Lyginopterideæ are the ancestral types of the Cycads (2). Chodat bases his criticism on the work of Bertrand and Cornaille (1) concerning the vascular system of living ferns, and is of the opinion that Scott's interpretation of the primary vascular structure of *Lyginopteris* needs revision. He believes that the so-called "mesarch" structure of the primary wood and leaf-traces of this plant is of a different nature from that of the petoliar bundles of Cycads; in fact, according to Chodat, *Lyginopteris* is merely a specialised fern having no particular relation with the Cycads. In that form (and *Heterangium*) the primary bundles of the stem, though apparently mesarch, are really endarch, the whole of the metaxylem developing centrifugally. The metaxylem becomes extended laterally, and then curves inwards in the form of an inverted omega (ω). The lateral extensions unite on the inner side of the protoxylem, enclosing it, together with a few parenchymatous cells, thus forming a closed "divergent"—a typically filicinean unit of vascular structure. In Cycads, however, the vascular bundles of the petiole are truly mesarch, consisting chiefly of centripetal xylem (except near the base of the leaf-stalk); the protoxylem is in connection with the centripetal xylem, and is usually separated from the centrifugal xylem by a few parenchymatous cells. According to Le Goc (6), the centrifugal xylem is largely secondary in origin (particularly at the base of the petiole), while the centripetal xylem is wholly primary; they are thus independent morphologically, though more or less secondarily connected for physiological reasons. Marsh (6a), however, while agreeing with Le Goc as to the nature of the centripetal and centrifugal xylem, maintains that there is a primary connection between them. The frequent presence of parenchymatous cells separating the centrifugal xylem from the protoxylem is due to the disappearance of the primary centrifugal elements. It is, at any rate, clear that if Chodat's conception of the primary wood of *Lyginopteris* be the correct one, the similarity between the bundles of this type and those of recent Cycads, as described by Messrs. Le Goc and Marsh, is only apparent; the difference in organisation between the two types is at once seen by a comparison of Figs. 132 and 133 in Scott's "Studies." As Weiss points out, "Chodat's criticism seems sufficiently weighty to demand a careful reconsideration of the structure and affinities of the Lyginodendreæ" (18, p. 6).

Turning to the second group of Pteridosperms, those of the Medullosean alliance, we find as its basal and simplest form *Sutcliffia insignis*, two specimens of which are at present known. The first specimen was described by Dr. Scott in 1906 (13, see also 14, p. 447), and in 1912, an account was given by Dr. de Fraine (3) of a second, evidently representing an older stage than the first. Both specimens are of Lower Coal Measure age. This species is considered to represent an important stock, so far as evolutionary tendencies are concerned.

In vascular anatomy, *Sutcliffia* is very similar in type to *Heterangium* (Fig. 6). There is a single stele without pith, the central part consisting of strands of tracheides mixed with conjunctive parenchyma. In *Sutcliffia*, however, the protoxylem groups are exarch, instead of mesarch as in *Heterangium*. The secondary xylem, the tracheides of which bear multiseriate pits, is locally very

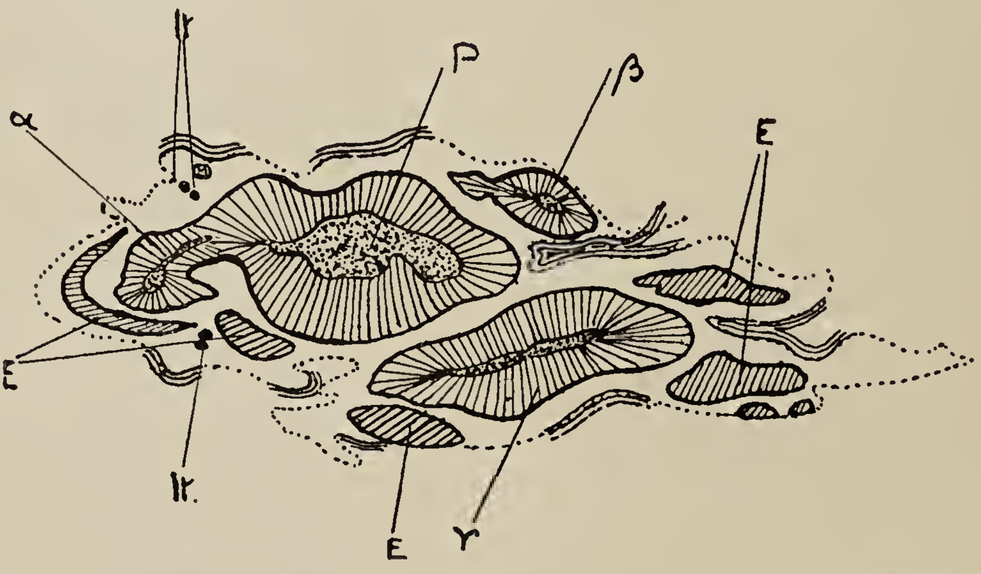


FIG. 6.—*Sutcliffia insignis*. Outline of vascular strands. The broken line represents the limit of the tissues; the triple lines represent arcs of secondary cortex. α, β, γ, meristeles; *P*, protostele; *E*, extrafascicular strands; *lt*, leaf-traces. (Adapted from de Fraine, 1912).

parenchymatous in nature, its texture being similar to that of the Cycads. The main differences from *Heterangium* consist in the presence of large accessory vascular strands ("meristeles") round the stele of the stem, and in the more complex vascular system of the petioles. The meristeles separate from the main stele, and are at first concentric in structure, being surrounded by secondary tissues. They divide repeatedly, forming either unilateral or radially symmetrical concentric foliar traces. The ultimate traces have no secondary tissue, this having been gradually lost. In Miss de Fraine's new specimen extrafascicular bands of wood and phloem, showing occasional inverse orientation, form a network round the stele and the leaf-strands. The vascular strands of the petioles belonging to *Sutcliffia* are concentric as in *Heterangium*, but they are numerous in each petiole, as in recent Cycads. The whole leaf-supply system is thus much more complicated than in *Heterangium*.

The evolutionary tendencies of the Medullosean alliance, like those of the Lyginopteridean group, seem to have found expression in progressive complication of the vascular system, for in all types except *Sutcliffia*, polystely prevails.

Medullosa anglica (11; 14, p. 428) represents so far as is at present known, the next stage to *Sutcliffia* in vascular evolution. It, also, is of Lower Coal Measure age. The stem, instead of being monostelic as in *Sutcliffia*, possesses three equivalent steles, each one having the same structure as the single stele of *Sutcliffia*, except that the protoxylems are mesarch (Fig. 7). A stele of *Medullosa anglica* is thus better compared with the stele of *Heterangium*. In

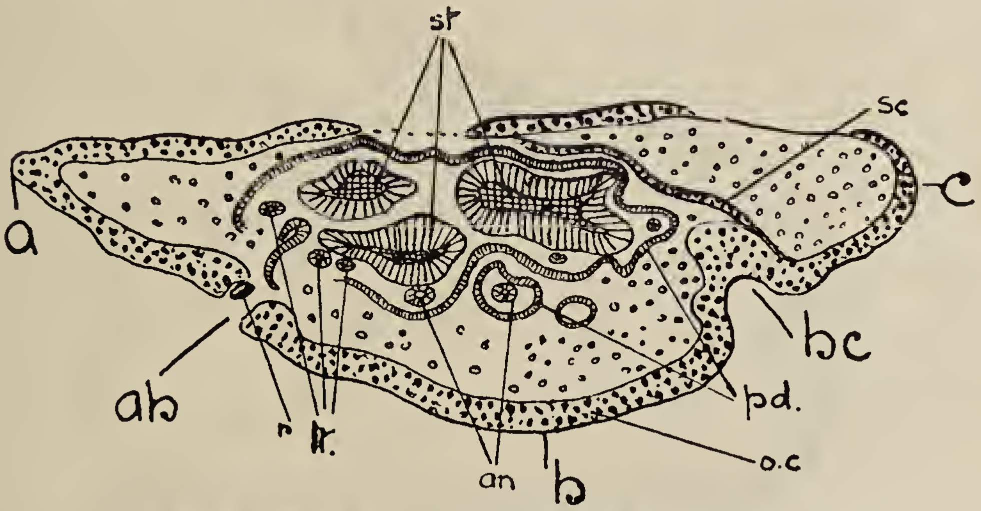


FIG. 7.—*Medullosa anglica*. Transverse section of stem, showing three large leaf-bases, *a*, *b*, and *c*. *ab*, *bc*, position of next leaf-bases above. *st*, the three steles; *lt*, leaf-traces; *an*, accessory rings of wood and bast; *pd*, periderm forming a ring round the group of steles, and also enclosing one of the accessory strands; *r*, adventitious root; *oc*, hypoderma; *sc*, sclerenchymatous band between leaf-base and stem. (After Scott, 1899).

fact, Dr. Scott describes *M. anglica* as having roughly the organisation of a polystelic *Heterangium* (14, p. 433). Occasionally, accessory vascular strands, of concentric structure, are to be found in the cortex; these are interesting in comparison with the similar cortical bundles occurring in some recent Cycads.

The foliar vascular supply is quite similar to, though perhaps less complicated than that of *Sutcliffia*. From the outer surfaces of the three stem-steles are given off large concentric bundles, each consisting of a central mass of mesarch primary wood, surrounded by secondary wood and phloem. During its outward passage, the leaf-trace divides repeatedly, losing its secondary tissues, and forming a group of small bundles each having exarch collateral structure.

Each leaf-base of *Medullosa anglica* receives seventy or eighty vascular bundles, these being the product of the division of several original leaf-traces. Where the petiole becomes free from the stem, the vascular system consists of numerous collateral vascular bundles, arranged more or less in groups corresponding to the leaf-traces from which they were derived (Fig. 8). The orientation of the bundles is scattered and irregular. The whole structure is very like that of the petioles of some recent Cycads, the chief point of difference being the absence of centrifugal wood. Sometimes, however, even this difference does not appear to exist. Petioles of this kind are known under the generic name of *Myeloxylon*.

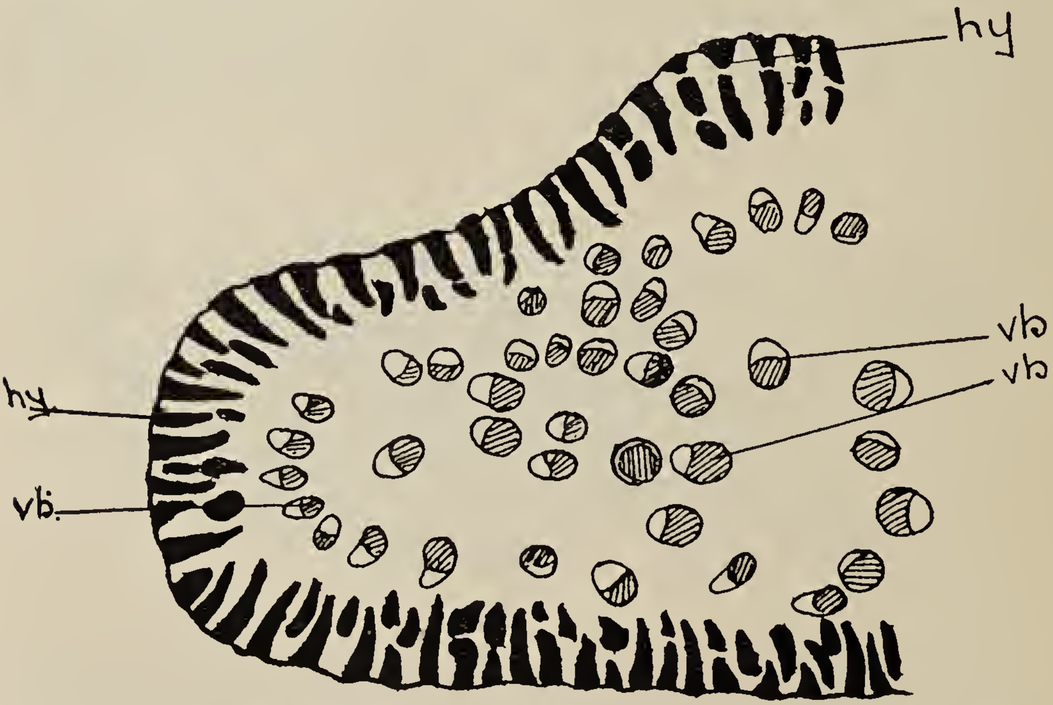


FIG. 8.—*Medullosa anglica*. Part of a transverse section of a petiole showing the numerous vascular bundles, *vb*; *hy*, hypoderma, with sclerenchymatous ribs. The whole has the structure of "*Myeloxylon Landriotii*." (Adapted from Scott, "Studies.")

At the British Association Meeting of 1913, Dr. de Fraine described a new species of *Medullosa*, obtained from the Lower Coal Measures (4). The vascular system of this specimen consists of three steles in the upper, and four in the lower part of the length of stem represented; these steles form an outer system which encloses a small central strand, this being the principal difference from *M. anglica*. The strand remains unchanged throughout the stem-fragment.

This new specimen forms a transition between *Medullosa anglica* and other species of the same genus more complicated in vascular organisation. These forms are continental and are obtained chiefly from the Permian beds of France and Germany, being thus of a later geological age than the two species described above. They possess numerous steles which apparently agree in structure with those of the English species. The steles are of two forms, *viz.*, "plate-rings," usually elongated tangentially and associated to form a single or double peripheral ring; and "star-rings," smaller and more rounded in transverse section, and grouped together in the central region of the stem.

It may be noted in passing that the vascular systems of the various types of the Medulloseæ are apparently paralleled amongst the Filicineæ, suggesting a similar mode of evolution (cf. 16), and it is an open question whether the terms employed in describing the vascular systems of ferns may not be used also in the case of Medulloseæ. For example, the single stele of *Sutcliffia* may be compared with the protostele of such a form as *Lygodium;* the continuous zone of vascular tissue in *Medullosa porosa* may be a solenostele derivable from a protostelic type; the arrangement of the two circles of plate-rings in *M. Solmsii* suggests both polycycly and dictyostely; while the "star-rings" in the central regions of many Medullosean stems, for example, *M. stellata*, may be merely accessory vascular strands of the same nature as those in *Cyathæa*. The fact, however, that polystely in Medulloseæ has no relation to the presence of leaf-gaps (14, p. 444) suggests that it is not of the same nature as that found in ferns, but that it has arisen within the family, from protostelic forms, perhaps, such as *Sutcliffia*. In the following descriptions therefore, the terms "plate-ring" and "star-ring," usually employed in reference to the vascular system of the Medulloseæ, will be retained.

Weber and Sterzel (17) have grouped the Continental Medulloseæ into "form-cycles," each consisting of a typical species and varieties which may or may not be quite distinct from the type. The form-cycles are those of *Medullosa stellata*, *M. porosa*, *M. Solmsii* and *M. Leuckarti*. A brief consideration of each one is necessary in view of the importance attached by various workers to the genus.

In *Medullosa stellata* (Fig. 9) the peripheral steles or plate-rings are few in number and are much elongated tangentially so that they collectively form an almost continuous ring with few interruptions. There are numerous star-rings, mostly large in size. The varieties of the type depend mainly upon the degree of continuity of the outer stelar system and on the variations in thickness of the wood on the inner and outer sides of this system; variety *gigantea*, however, presents an additional complication in the development of

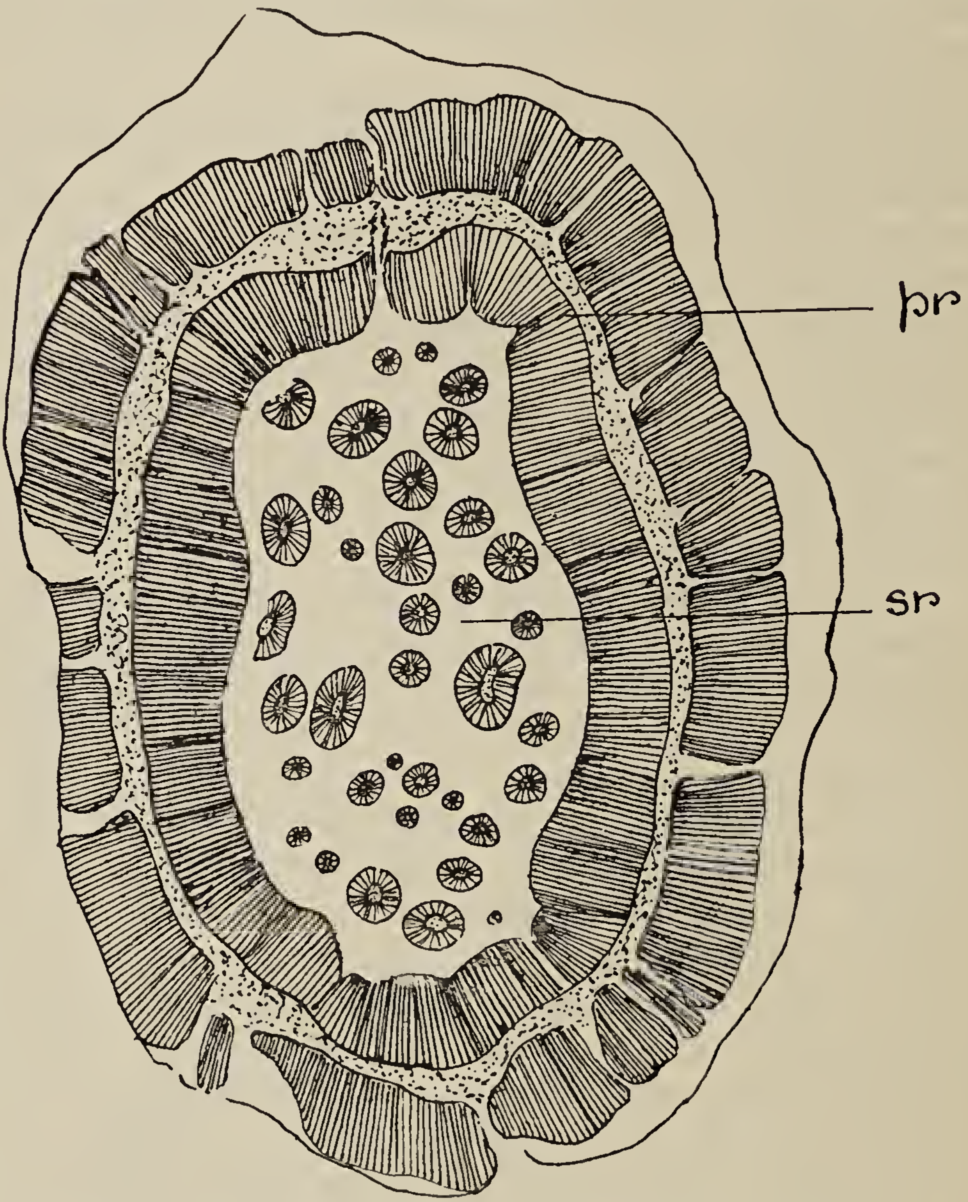


FIG. 9.—*Medullosa stellata* v. *typica*. Transverse section of stem, showing *pr*, peripheral vascular system; and *sr*, star-rings of the medullary system. (Adapted from Weber and Sterzel, 1896).

three zones of normally orientated xylem and phloem *outside* the ordinary peripheral system, just as in some recent Cycads there is a development of extrafascicular zones of vascular tissues.

Medullosa porosa (Fig. 10) and its varieties are very similar to *M. stellata*. In this case, the peripheral vascular system forms an unbroken, or only incompletely broken ring, like a solenostele. The outer medullary- or star-rings are often incompletely surrounded by secondary wood, this indicating a tendency towards reduction of the concentric steles to form collateral bundles—an important tendency, when a comparison is made with recent Cycads, according to Worsdell.

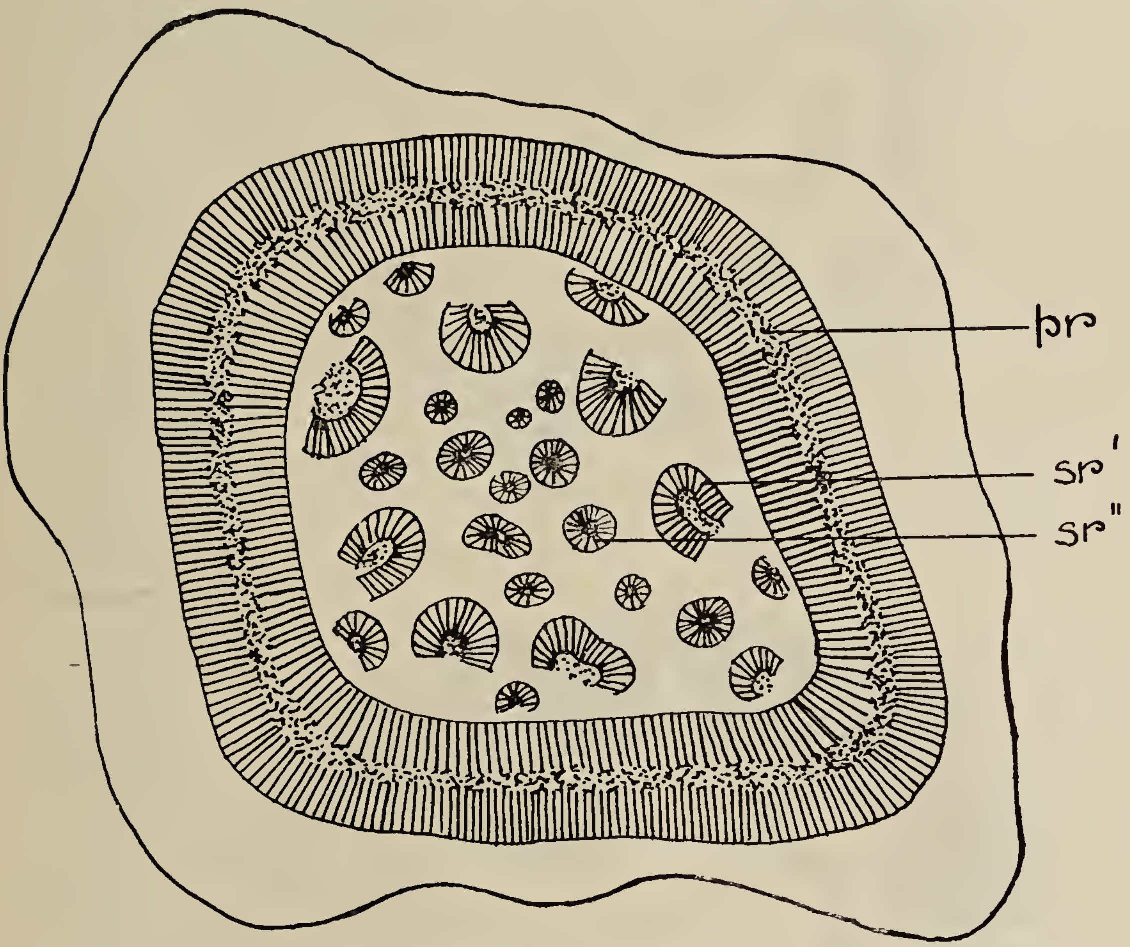
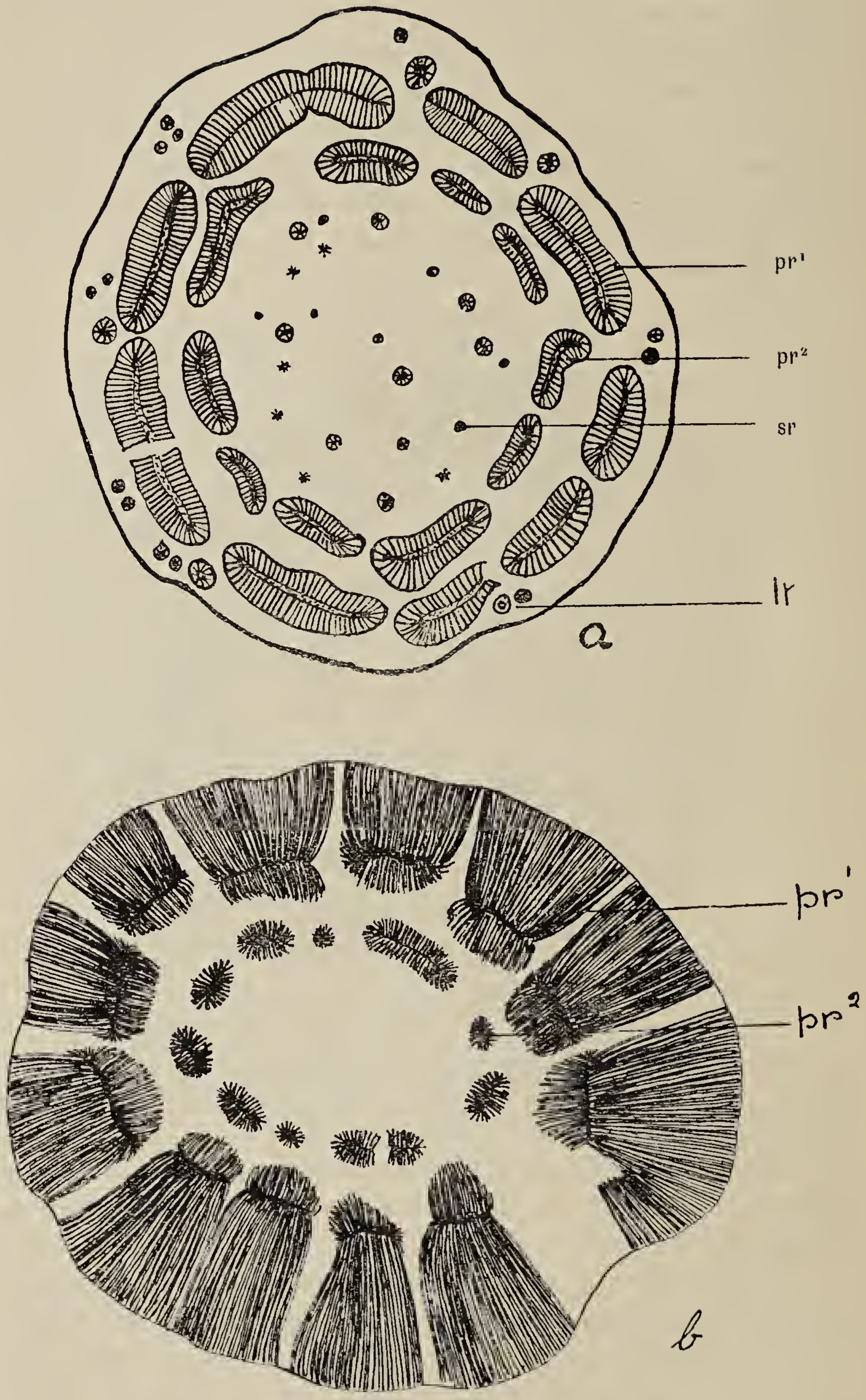


FIG. 10.—*Medullosa porosa* v. *typica*. Transverse section of stem, showing *pr*, the unbroken peripheral vascular system; *sr'*, the outer series of star-rings with incomplete development of secondary tissues; *sr"*, the inner star-rings. (Adapted from Weber and Sterzel, 1896).

In the form-cycle of *Medullosa Solmsii* (Fig. 11), the peripheral system consists of two zones of plate-rings. There are usually numerous very small star-rings. The variations depend chiefly upon the differences in development of the normal and inverse xylem of the outer plate-rings. In variety *lignosa* (Fig. 11, *c*), there are several consecutive zones of normally orientated wood and phloem as in *M. stellata* v. *gigantea* and some recent Cycads.



(For continuation and description of Fig. 11 see page 57).

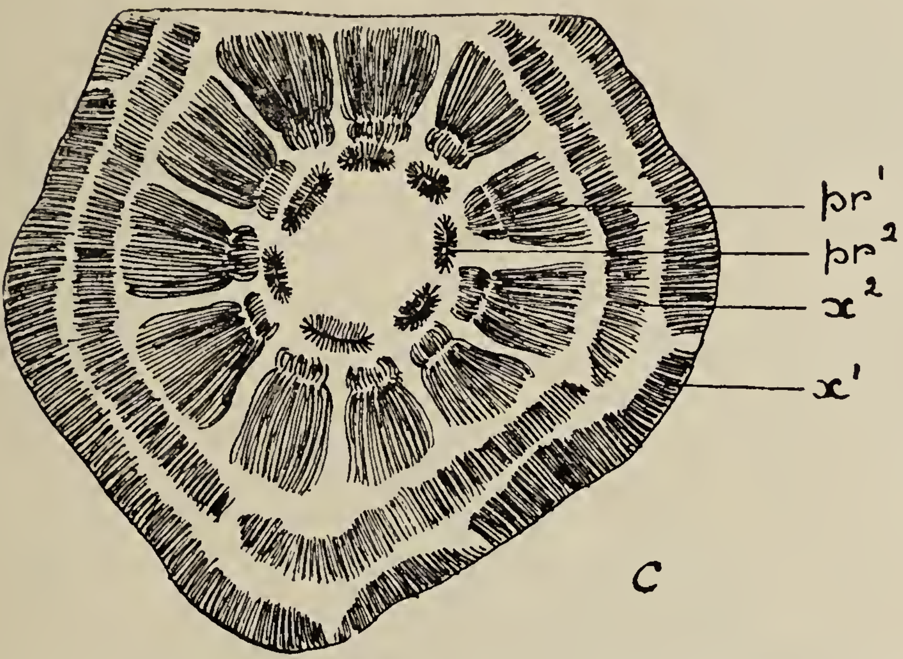


FIG. 11.—*Medullosa Solmsii.* A, v. *typica.* *pr*¹, outer plate rings; *pr*², inner plate-rings; *sr*, star-rings; *lt*, leaf-trace. B, v. *incrassata.* C, v. *lignosa.* *x*¹ and *x*², normally orientated extra vascular zones. (Adapted from Weber and Sterzel, 1896).

Finally, *Medullosa Leuckarti* (Fig. 12) possesses a peripheral vascular system consisting of one or several series of plate-rings, each much elongated tangentially. The star-rings are rather large and quite concentric.

In those cases amongst the Continental Medulloseæ where the petioles are known, they are of the *Myeloxylon* type, so that the likeness of the petioles to those of recent Cycads noted in *M. anglica* is constant, so far as is known.

Several other genera belonging to the family Medulloseæ need not concern us here, *Sutcliffia* and the various species of *Medullosa* only, being of particular interest in a consideration of the derivation of Cycadean anatomy.

As mentioned above, Worsdell is a vigorous exponent of the view that Cycadean anatomy has been derived from the polystelic Medulloseæ, this theory having been formulated before the discovery of the monostelic type, *Sutcliffia.* It was first advanced by Potonié in 1899 (9, p. 168), but was stated independently and extended by Worsdell (23) some years later. Chodat (2, p. 38) more recently has supported the theory, considering the agreement of the Medulloseæ with the Cycadaceæ to be so close that he regards them as Protocycadeæ. Scott, on the other hand, considers that the polystelic structure of the Medulloseæ other than *Sutcliffia* (which, he says, "does not affect the question" (14, p. 649)), distinguishes them from the recent and Mesozoic Cycadophyta, which are to be regarded as monostelic; he explains the additional vascular cylinders of some recent Cycads as being "local peculiarities in the vascular system due to anomalous distribution of the cambium"; they are therefore of no phylogenetic significance.

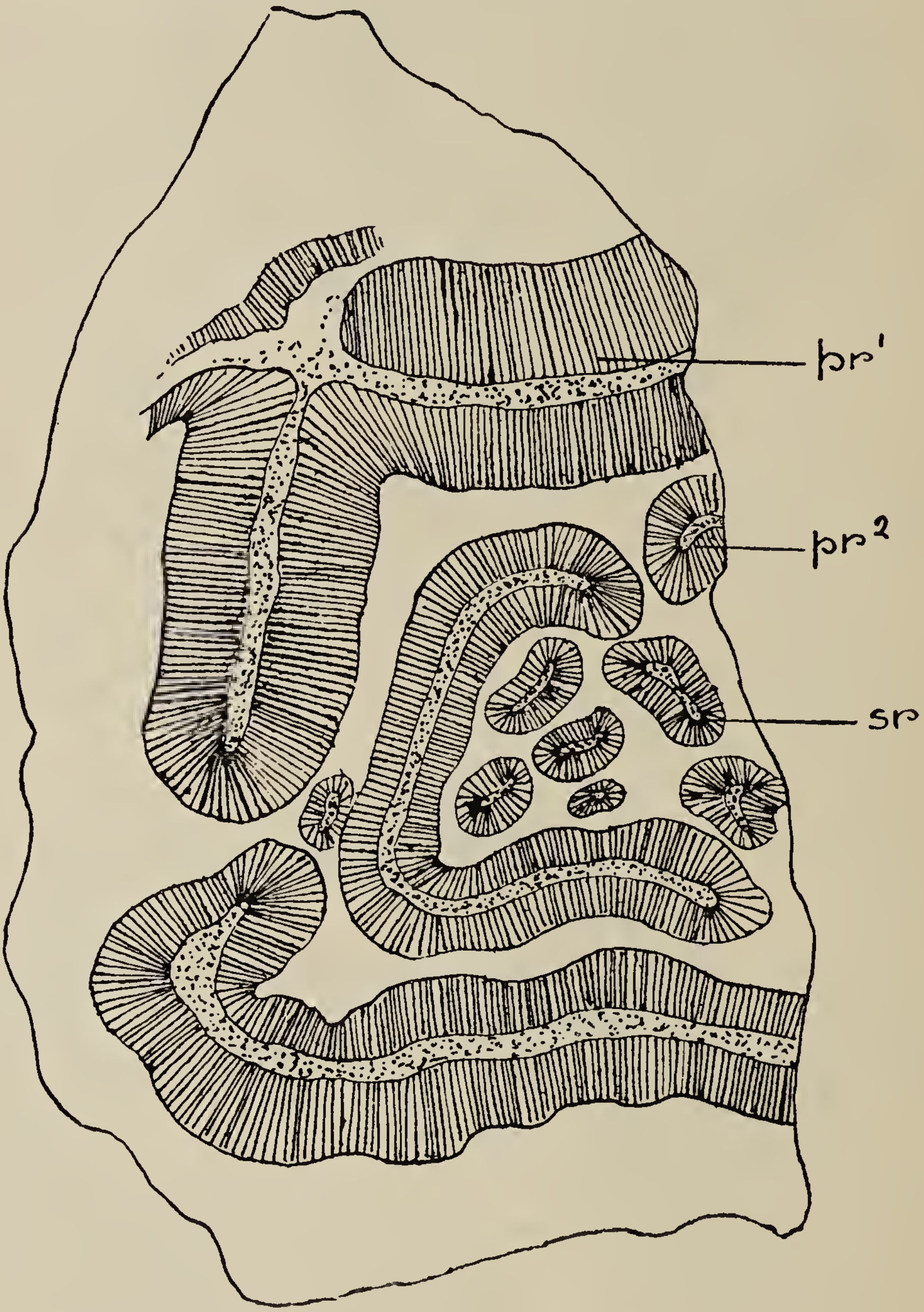


FIG. 12.—*Medullosa Leuckarti.* Transverse section of part of stem. *pr*¹, first peripheral vascular system; *pr*², second peripheral system; *sr*, medullary system of star-rings. (Adapted from Weber and Sterzel, 1896).

According to Worsdell, the normal vascular system of Cycads consists of "the one-sided remnants of a number of steles"; and the so-called anomalous vascular structures in some genera are all that remain of concentric cylinders, normal in an ancestral type. Worsdell bases his theory of the Medullosean ancestry of Cycads upon evidence derived from a consideration of vascular structure (*a*) in the cotyledonary node, where, he considers, ancestral traits are likely to be found in the earliest vascular tissues; and (*b*) in the flowering axis, for it is held that here the vascular tissue will have undergone less modification on account of conduction than is the case with the vegetative stem.

With regard to the first point, Worsdell believes that the cotyledonary node of certain Cycads exhibits structural peculiarities which indicate, to a great extent, the origin of the vascular structure as a whole. *Cycas siamensis* (7; Fig. 13), *Cycas Seemanni* (5; 22), *Cycas revoluta* (20), *Encephalartos horridus* (21), *Macrozamia Denisonii* (22), and *Bowenia spectabilis* (22) show concentric vascular strands surrounding the main axis. These give the seedlings an appearance of polystelic structure in this region, constituting the first extra-fascicular ring. Worsdell believes them to be the remnants of an ancestral solenostelic or polystelic structure derived from such a form as *Medullosa porosa* or *Medullosa Leuckarti*.

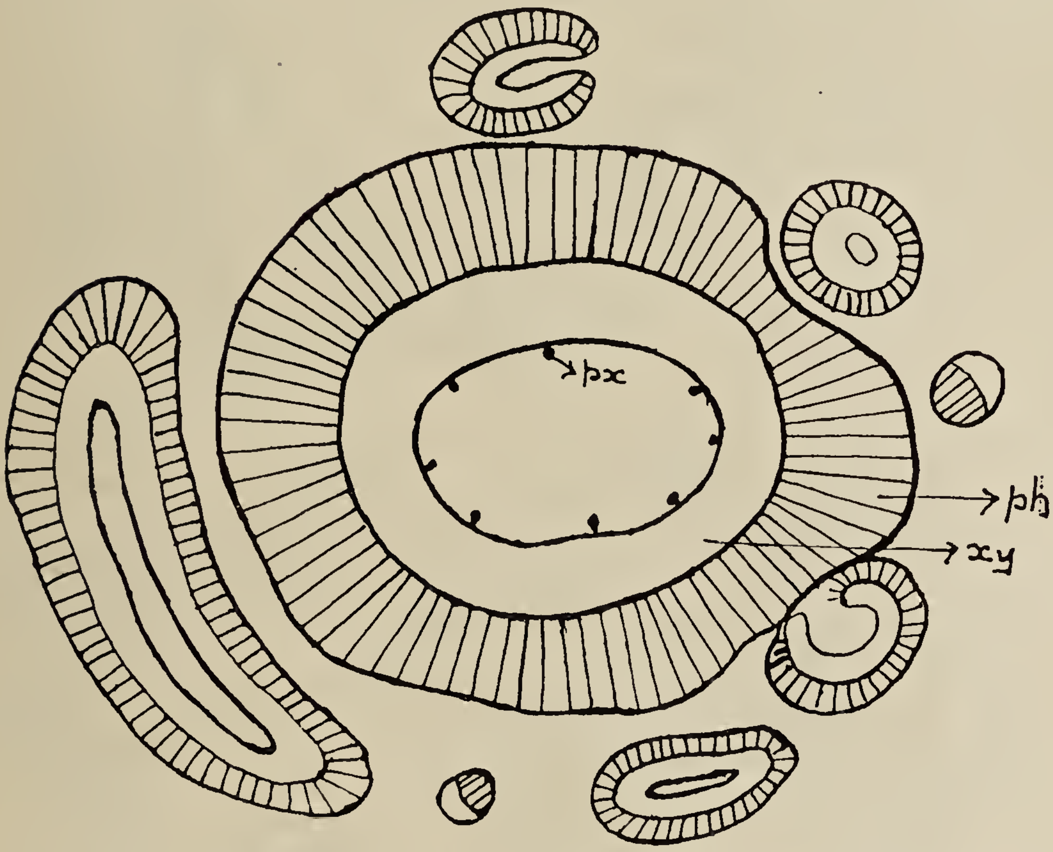


FIG. 13.—*Cycas siamensis*. Transverse section of vascular system of seedling-axis in region of cotyledonary node, showing outer ring of steles. (Adapted from Worsdell, 1906, after Matte).

A seedling of *Encephalartos Barteri* described by Matte (7) shows three almost independent steles in place of the usual endarch cylinder (Fig. 14). Worsdell, in complete agreement with Matte, considers this structure as being of considerable phylogenetic significance, comparable with the three steles of *Medullosa anglica*.

In the basal region of a young stem of *Macrozamia Denisonii* (22), concentric strands were seen to occur immediately outside the central cylinder; in the same region of a mature stem of *Macrozamia Fraseri* the concentric strands were represented by bands of normally orientated elements, showing here and there traces of their ancestral condition in the presence of small inverted strands on their inner side. In the primary node of the stem of *Cycas Seemanni* (22), the first extrafascicular ring was composed of concentric strands; this was followed by a continuous zone with collateral

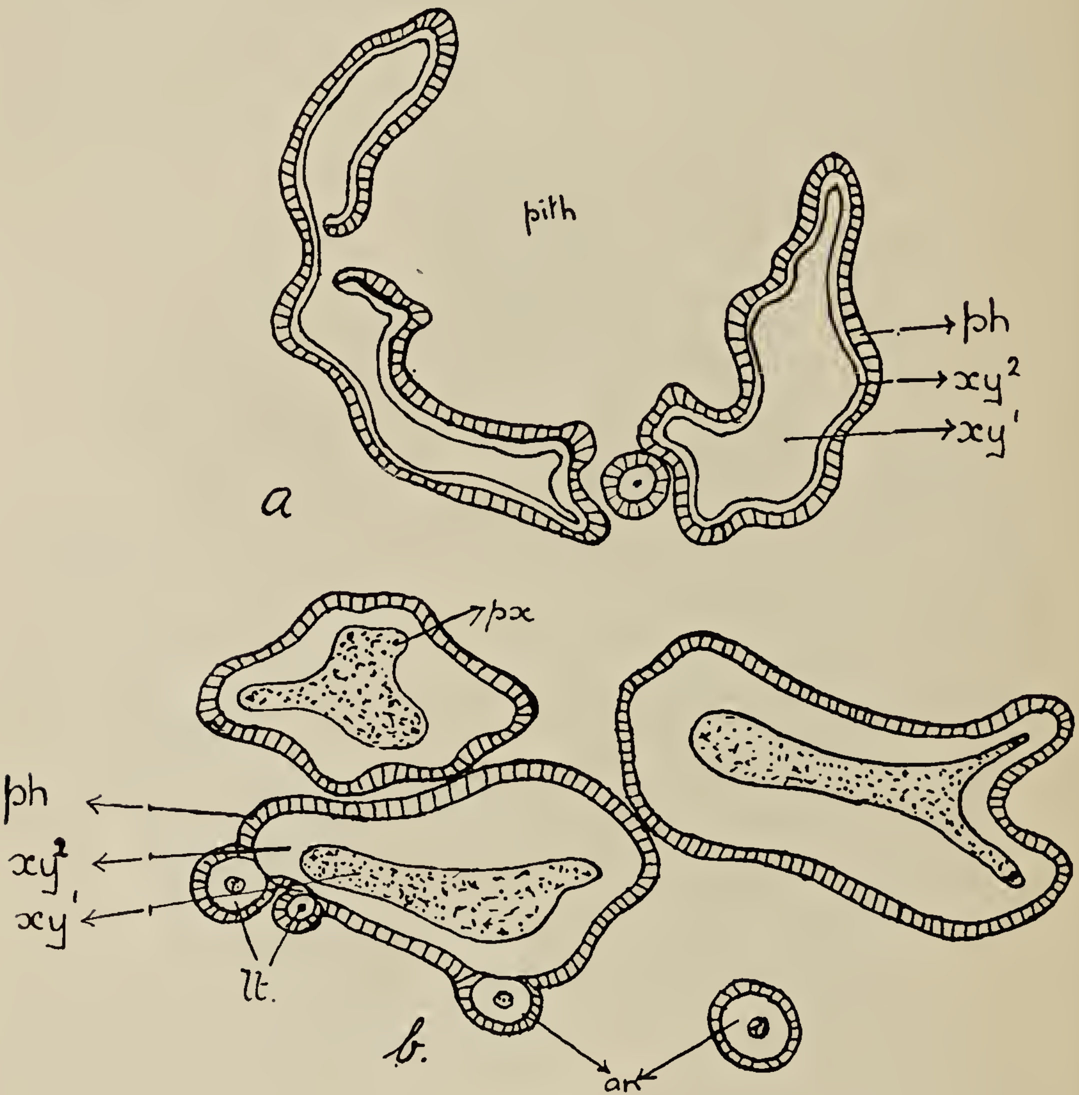


FIG. 14.—A, *Encephalartos Barteri*. Transverse section of the seedling-axis in the region of the cotyledonary node, showing the medullosa-like steles. (Adapted from Worsdell, 1906, after Matte). Cf. *Medullosa anglica*.

B, *Medullosa anglica*. Transverse section of the vascular system of the stem, showing three main steles, two anomalous steles and two leaf-traces. (Adapted from Worsdell, 1906, after Scott).

*xy*¹, central primary xylem; *xy*², secondary xylem; *ph*, phloem; *lt*, leaf-traces; *an*, anomalous steles.

structure (Fig. 15, *b*). In another plant, at a slightly lower level (Fig. 15, *a*), the first extrafascicular ring consisted of an interrupted collateral zone; second and third rings also occurred with traces of inverse bundles indicating, according to Worsdell, the solenostelic origin of the rings. *Medullosa stellata* v. *gigantea* and *Medullosa Solmsii* v. *lignosa* are of interest in comparison with these cases, for they had already "advanced very far in the modern Cycadean

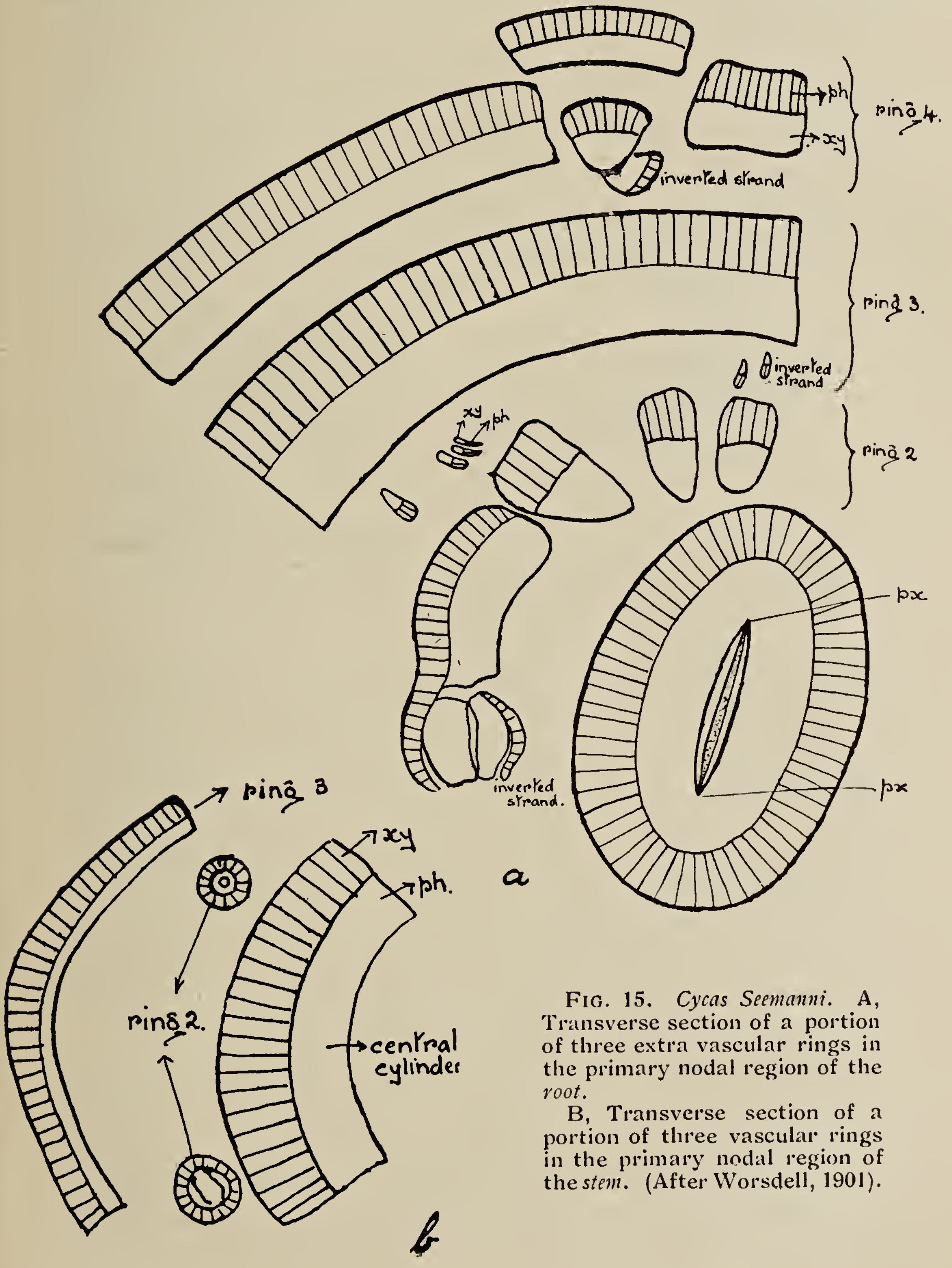


FIG. 15. *Cycas Seemanni*. A, Transverse section of a portion of three extra vascular rings in the primary nodal region of the *root*.

B, Transverse section of a portion of three vascular rings in the primary nodal region of the *stem*. (After Worsdell, 1901).

direction by adopting a collateral structure" in their extrafascicular rings.

In the primary node of *Macrozamia Denisonii* (22), there are cortical cauline strands wholly or partly concentric. Worsdell believes these to be homologous with the anomalous concentric strands in *Medullosa anglica* and with the extrafascicular strands figured by Weber and Sterzel (17, see Taf. iv, Fig. 2, *b*) in *Medullosa Leuckarti* (Fig. 16).

In *Medullosa Solmsii* and *Medullosa Leuckarti*, it will be remembered, there are two primary rings of steles, those of the innermost ring being smaller and less well-organised than those of the outer. *Medullosa porosa* also possesses an inner ring, the steles of which may have been derived from the medullary system. "In fact, transitions exist between the medullary system and the inner cylindrical system of steles." Worsdell is convinced "that in the Medulloseæ, the cylindrical and medullary systems are merely *variants of a single system*"; either the cylindrical system has been formed by the regular annular grouping of the outermost members of a system of scattered steles, in which case the medullary strands would represent the primitive arrangement: or, the medullary steles have been derived from a primitive cylindrical system. According to Worsdell, the latter alternative is the most tenable.

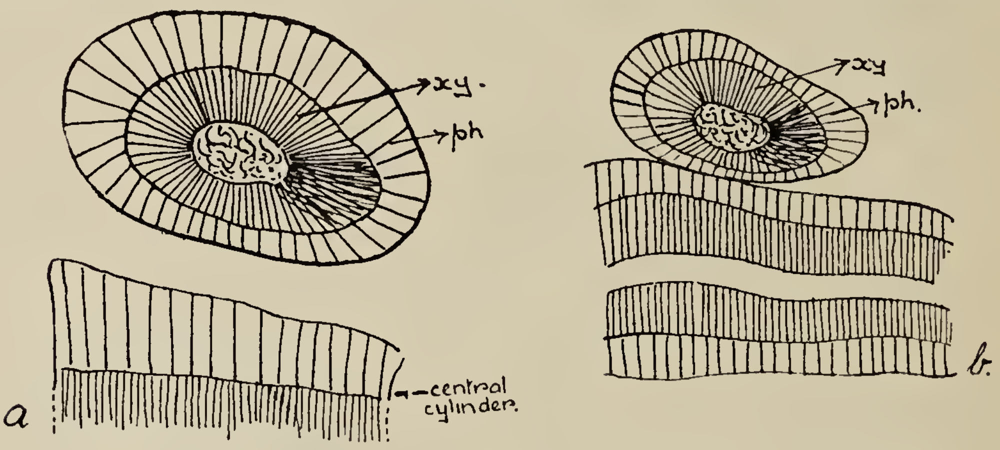


Fig. 16.—A, *Macrozamia Denisonii*. Transverse section of concentric cortical strand, just outside the central cylinder of primary node. cf. *Medullosa Leuckarti*. B, *Medullosa Leuckarti*. Transverse section of concentric strand outside the central cylinder of the stem. (Adapted from Worsdell, 1901).

Usually the medullary steles are concentric in structure, but those in *Medullosa porosa* show various stages of reduction towards the collateral type, orientation being irregular.

The medullary system of *Encephalartos* and some Macrozamias is comparable with the medullary system in *Medullosa*, being of the same system as the vascular rings.

With regard to Worsdell's second point—a consideration of the flowering axis of recent Cycads:—In the upper part of the peduncle of *Stangeria*, the vascular bundles become very irregularly orientated; some are more or less curved or even concentric. Worsdell considers that these bundles are the result of fragmentation of two or three sinuous steles, such as those of *Medullosa Leuckarti* (Fig. 17); the type of stele in *M. Solmsii* would represent an intermediate stage in fragmentation. Further, the centripetal

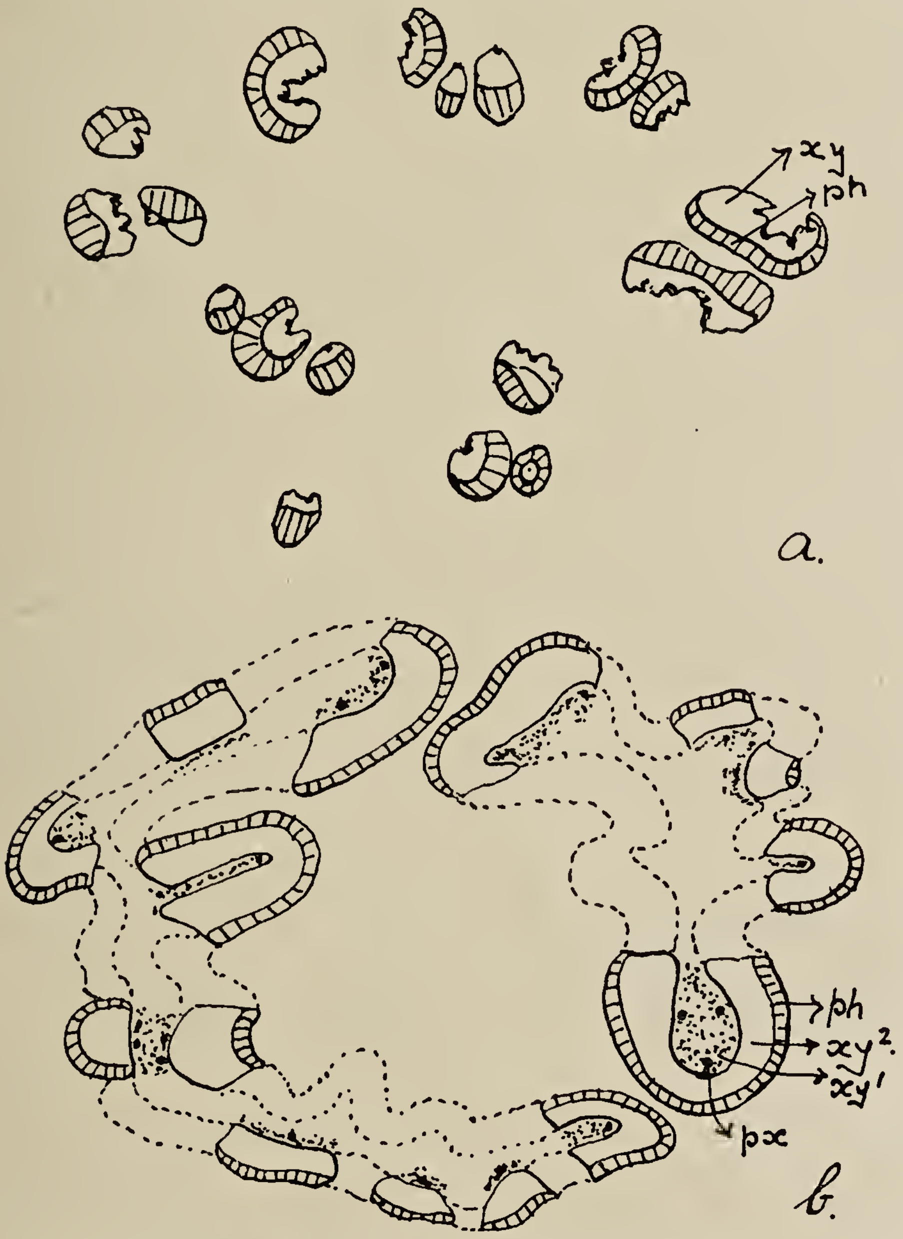


FIG. 17.—A, *Stangeria paradoxa*. Transverse section of lower region of peduncle, showing irregular orientation of bundles. (Adapted from Worsdell, 1906, after Scott). cf. *Medullosa Leuckarti*.

B, *Medullosa Leuckarti*. Transverse section of the vascular system of the stem, schematically drawn to represent how the vascular system of *Stangeria* could have been derived by fragmentation of the large irregularly-shaped steles, the dotted lines representing the eliminated portions. (Adapted from Worsdell, 1906).

xylem which appears later in these *Stangeria* bundles is held by Worsdell to be an ancestral character. He regards it as being usually the homologue of the central part of such a stele as that of *Medullosa anglica*, though it may correspond to the oppositely orientated xylem of the original strand. Scott, as we have seen, believes that the centripetal xylem, as found in the peduncle of *Stangeria* and other Cycads is the homologue and derivative of the centripetal primary xylem (if it be centripetal!) occurring in the bundles of the vegetative stems of *Lyginopteris* and *Heterangium*. In this, of course, Worsdell and Scott agree, but they differ as to the mode of origin of the vascular tissue in these fossil plants. According to Scott, the centripetal xylem of *Lyginopteris* is all that remains of the mass of primary xylem, which, with conjunctive parenchyma, occupies the centre of the *Heterangium* stele. Worsdell, on the contrary, holds that in *Lyginopteris* each primary xylem group with its accompanying secondary centrifugal xylem and phloem is "the one-sided remnant of an *entire stele* or *concentric bundle*, and is hence precisely comparable to, and homologous with, each bundle in the peduncle of *Stangeria*" and other forms; in both cases, the ancestral form of vascular structure would be a stele like one of those of a Medullosean stem. His reasons for so believing depend largely upon the sinuous contour of the secondary xylem in *Lyginopteris* indicating its compounded character (Fig. 18, *a*); and upon the formation of concentric strands of vascular tissue in place of the ordinary bundles of the stem, by the growth of the cambium through the leaf-gaps (Fig. 18, *b*), which Worsdell regards as a reversion to an ancestral character. So that, according to him, not only is the Cycadean vascular system traceable to an origin amongst polystelic types, but that of *Lyginopteris* also.

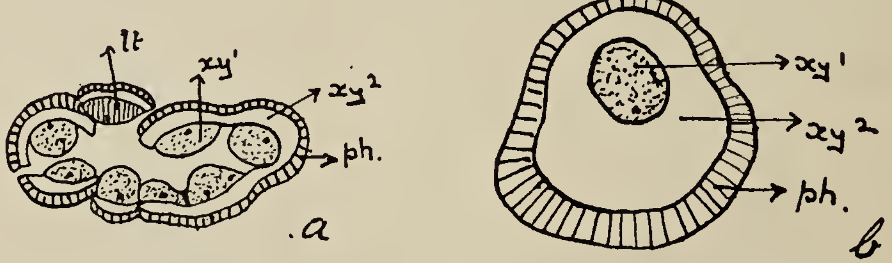


FIG. 18.—*Lyginopteris oldhamia*. A, transverse section of vascular ring of stem of young plant. (Adapted from Worsdell, 1906, after Williamson and Scott).

B, transverse section of single bundle from vascular ring of stem, showing its concentric stele like structure, caused by extension of the cambium through leaf-gaps. (After Worsdell, 1906).

The fertile portions of the axis of the male cone in *Ceratozamia mexicana* and *Ceratozamia latifolia* exhibit the rudiments of an intra-fascicular primary cylinder of bundles. These bundles are feebly-developed and are scattered and variously orientated, or concentrically grouped. Worsdell regards this inner series as the remnants of the inner cylinder of primary bundles in some Medulloseæ. Similarly in the peduncle of *Encephalartos* there are two primary cylinders, the outermost being divided into groups of concentrically-arranged bundles (Fig. 19).

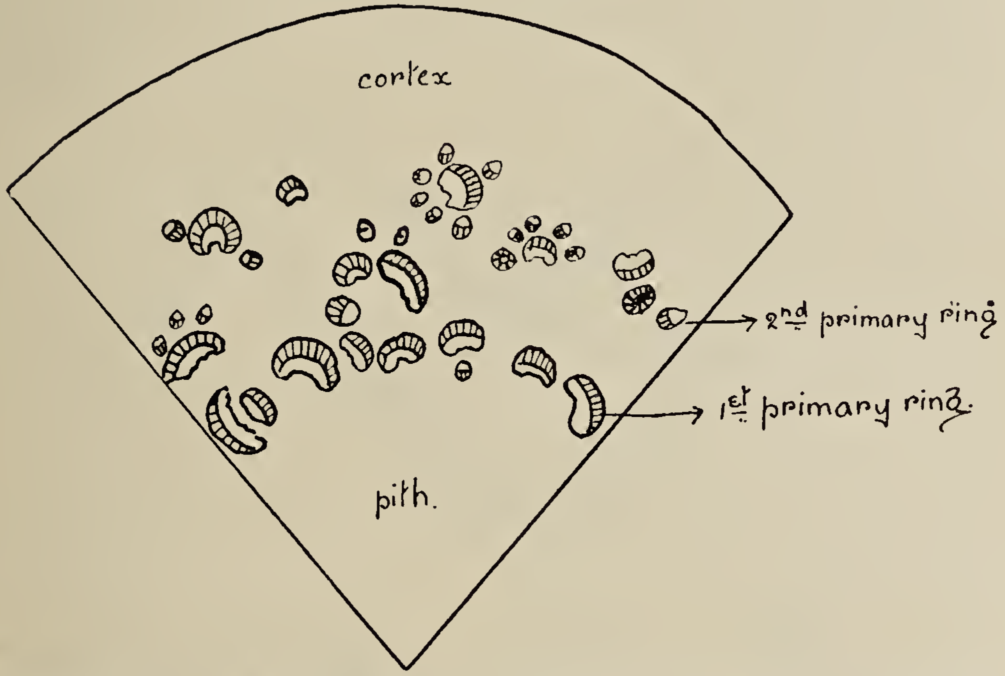


Fig. 19.—*Encephalartos villosus.* Transverse section of part of vascular system of peduncle, showing outer primary ring consisting of groups of bundles. (From Worsdell, 1906, after Matte).

Briefly considering the support for Worsdell's theory derived from a study of the foliar organs:—A comparison of the petiolar structure of *Encephalartos* and *Myeloxylon* shows that in the two types the structure, orientation and number of the vascular bundles are so similar as to indicate that the petiolar vascular systems of the recent and fossil forms are homologous. Further, Worsdell shows how a relation may exist between the vascular systems of the petioles of *Lyginopteris* and *Heterangium* on the one hand, and of Medulloseæ or Cycads on the other. The (usually) single large mesarch bundle of *Lyginopteris* may represent "a number of collateral mesarch bundles united by means of their centripetal xylems," their fused phloems surrounding the whole. If these bundles become separate, while retaining their original position, the grouping so characteristic of Cycad petioles, particularly of *Stangeria*, is obtained (Fig. 20). *Myeloxylon* and some species of *Encephalartos* may represent extreme cases of sub-division of an original vascular strand. Cases of fusion in Cycad petiolar bundles may be regarded as a reversion to an ancestral condition.

Since Worsdell formulated his theory of the Medullosean origin of Cycadean vascular structures, the discovery of *Sutcliffia* has shed new light on the Medulloseæ as a group, showing that it possessed monostelic forms within itself. The description of the new form has carried with it a new view of the origin of the Cycads. A tentative statement was made by Scott in the concluding chapter of the "Studies" to the effect that "on the whole of the evidence available it appears likely that some at least of the Cycadophyta may have been derived from plants resembling the Medulloseæ (Neuropterideæ) in certain characters, though probably with monostelic rather than polystelic structure of the stem" (14, p. 650). Miss de Fraine has elaborated this view, at the same time criticising Worsdell's theory (3). She points out that in the light of recent research, reliance for ancestral characters upon the structure of the cotyledonary node and flowering axis is inadvisable; and concludes that the origin of Cycads from polystelic ancestors is "not yet satisfactorily proved." Miss de Fraine suggests as an

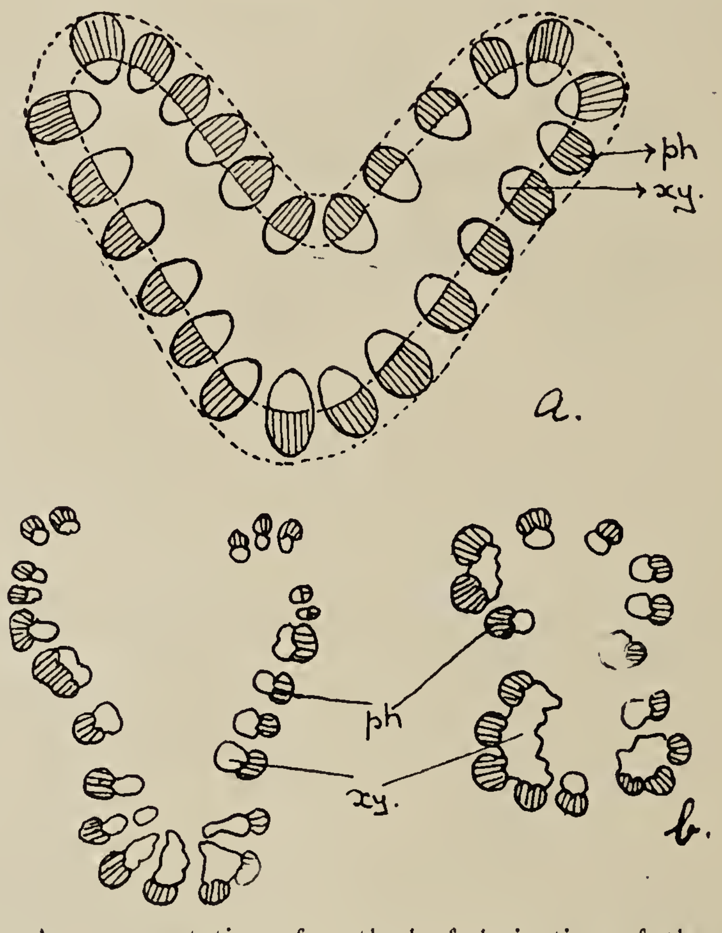


FIG. 20.—A, representation of method of derivation of the numerous, separate, collateral bundles of petiole of Cycads from the single large concentric bundle of petiole of *Lyginopteris*, etc. (transverse section). (After Worsdell, 1906).
B, *Stangeria paradoxa*. Transverse section of vascular system of petiole, showing lateral fusion of bundles. cf. grouping of bundles in A. (From Worsdell, after Matte).

alternative view that the central cylinder of a Cycadean stem may have been derived from a protostelic type such as *Sutcliffia*, the internal tracheides having been gradually lost. The extrafascicular zones and accessory cortical strands of some Cycads occur also in *Sutcliffia* and *Medullosa*, but it is at present impossible to determine whether they are connected with the original central cylinder, or whether they have arisen secondarily to meet physiological needs. Miss de Fraine considers that from such a primitive type as *Sutcliffia* two divergent lines of evolution may have arisen. The first line proceeded through fairly simple types like *Medullosa anglica* to complex types with numerous steles, and here ended blindly, for these types were evidently insufficiently plastic for further evolution to take place. The second line remained protostelic throughout, the original vascular system becoming modified and giving rise to the Cycadean type. In the case of polyxylic Cycads, the so-called anomalous vascular structures may have been derived by the elaboration of the extrafascicular arcs and accessory vascular strands of the ancestral type. Or, it might be suggested that in those recent Cycads which exhibit extrafascicular formations, it is merely a case of the expression of tendencies inherited from an ancestor which also gave rise to lines exhibiting the character constantly.

Miss de Fraine's view is interesting in that it derives Cycadean anatomy from a monostelic form very similar to *Heterangium*, the basal form of the line through which it has its origin according to Dr. Scott, who himself suggests the probability of a common origin of the Lyginopterideæ and Medulloseæ "from a point not very far below the level of stems such as those of *Sutcliffia* and *Heterangium*." So that since the discovery of *Sutcliffia*, which connects the two lines anatomically, the divergent theories of Scott and Worsdell are, to a certain extent, brought together by that of Miss de Fraine.

Also, the discovery of *Sutcliffia* adds further interest to the conclusion previously arrived at by Matte, to the effect that the Cycads were derived from the Lyginopterideæ or a nearly related family *through* the Medulloseæ. The existence of *Sutcliffia* to a certain extent, justifies this view, since it shows how nearly related are the two main groups of Pteridosperms.

From the evidence at present before us, it seems safe to suggest that the Lyginopterideæ and the Medulloseæ have arisen from a basal stock, giving origin also to the Cycadean line, this passing at least close to the simpler forms of the Medulloseæ.

BOTANY SCHOOL, CAMBRIDGE. *December, 1913.*

LIST OF REFERENCES.

1. Bertrand, C. E., et Cornaille, F. "La masse libéro-ligneuse élémentaire des Filicinées actuelles." Travaux et Mémoires de l'Université de Lille, t. X. mém. 29, 1902.

2. Chodat, R. "Les Ptéropsides des temps paléozoïques; étude critique." Arch. des Sci. phys. et nat., t. XXVI, 1908.

3. de Fraine, E. "On the Structure and Affinities of *Sutcliffia*, in the Light of a Newly Discovered Specimen." Ann. of Bot., vol. XXVI, 2, p. 1031, 1912.

4. ——— "A new Species of *Medullosa* from the Lower Coal Measures." (Abstract), British Association, Section K, 1913.

5. Gregg, W. H. "Anomalous Thickening in the Roots of *Cycas Seemanni*." Ann. of Bot., vol. I, p. 63, 1887.

6. Le Goc, M. J. "The Centripetal and Centrifugal Xylem in the Petiole of Cycads." (Abstract), British Association, Section K, 1913. Ann. of Bot., Vol. XXVIII, p. 183, 1914.

6a. Marsh, A. S. "Notes on the Anatomy of *Stangeria paradoxa*." New Phyt., Vol. XIII, p. 18, 1914.

7. Matte, H. "Recherches sur l'appareil libéroligneux des Cycadacées." Caen, 1904.

8. Oliver, F. W. "On *Physostoma elegans*, Williamson, an archaic type of Seed from the Palæozoic Rocks." Ann. of Bot., vol. XXIII, p. 73, 1909.

9. Potonié, H. "Lehrbuch der Pflanzenpalæontologie," 1899.

10. Renault, B. "Bassin Houiller et Permien d'Autun et d'Epinac, Flore fossile." Pt. II, 1896.

11. Scott, D. H. "Structure and Affinities of Fossil Plants from the Palæozoic Rocks. III: On *Medullosa anglica*, a new Representative of the Cycadofilices." Phil. Trans. Roy. Soc. B., vol. CXCI, 1899.

12. ——— "The Old Wood and the New." New Phyt., vol. I, p. 25, 1902.

13. ——— "On *Sutcliffia insignis*, a new Type of Medulloseæ from the Lower Coal Measures." Trans. Linn. Soc., vol. VII, p. 45, 1906.

14. ——— "Studies in Fossil Botany." 2nd ed., Pt. II, 1909.

15. Seward, A. C. "A Contribution to our knowledge of *Lyginodendron*." Ann. of Bot., vol. XI, p. 65, 1897.

16. Tansley, A. G. "Lectures on the Evolution of the Filicinean Vascular System." New Phyt., Vols. VI and VII, 1907, 1908.

17. Weber, O., und Sterzel, J. T. "Beiträge zur Kenntniss der Medulloseæ." Ber. der Naturw. Ges. zu Chemnitz, vol. XIII, 1896.

18. Weiss, F. E. Presidential Address to the British Association for the Advancement of Science, Section K, Portsmouth, 1911.

19. Williamson, W. C., and Scott, D. H. "Further Observations on the Organisation of the Fossil Plants of the Coal Measures. Part III: *Lyginodendron* and *Heterangium*." Phil. Trans. Roy. Soc., vol. 186, B, p. 703, 1895.

20. Worsdell, W. C. "The Comparative Anatomy of Certain Genera of the Cycadaceæ." Journ. Linn. Soc., vol. XXXIII, 1898.

21. ——— "The Comparative Anatomy of Certain Species of *Encephalartos*." Trans. Linn. Soc., vol. V, 1900.

22. ——— "Contributions to the Comparative Anatomy of the Cycadaceæ." Trans. Linn. Soc., vol. VI, 1901.

23. ——— "The Structure and Origin of the Cycadaceæ." Ann. of Bot., vol. XX, p. 129, 1906.

NOTE ON THE "FRUITING MALE" OF *PHŒNIX DACTYLIFERA* L.

By H. Martin Leake.

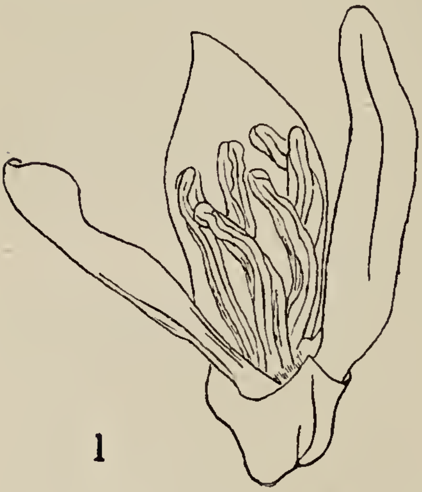
[With Five Text-Figures.]

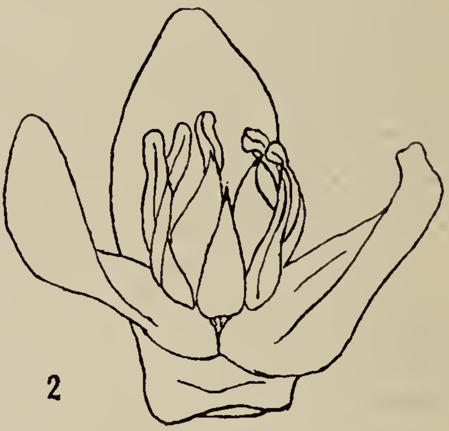
THE date palm, *P. dactylifera* L., is normally dioecious. The occurrence of so-called "fruiting males" is not, however, unknown. One such instance, occurring in Portugal, is recorded in Gard. Chron. '87, II, p. 530; in this case the male plant is stated to have produced a female inflorescence. Other cases are recorded by Toumey, Bull. 29, Arizona Exp. Sta.; Charlet, Bull. Soc. Geog. d'Alger. 1905; Kearney, U.S. Dep. of Agr. Bur. of Plant Industry No. 92; and Bois, Rev. Hort. 82 (10), p. 492.

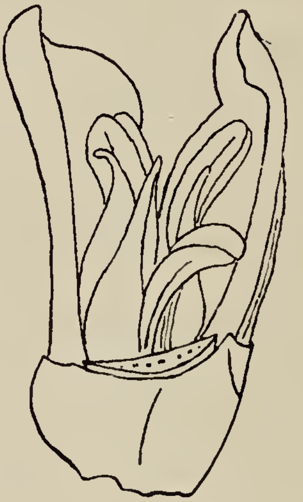
Kearney writes "The writer saw in February a palm which had all the characters of a male . . . . Nevertheless it bore clusters of small seedless dates . . . . . . Although the only case observed by him, this is apparently a rather well-known phenomenon." Bois cites an instance of a plant in which a certain number of flowers, on an inflorescence, in other respects typically male, develop fruits.

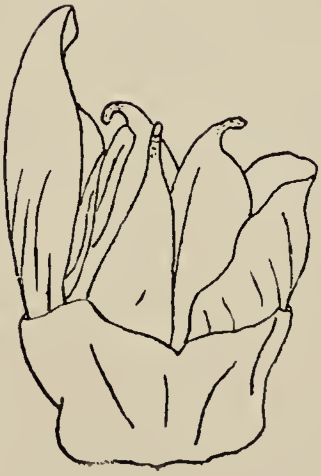
In all cases it is assumed that the change is from a dioecious, to a monoecious, habit. The observations have apparently been made on the plant when in fruit and there appears to be no record of the details of the flower-structure in such a plant. It may, therefore, be of interest to give in greater detail a further instance of this phenomenon.

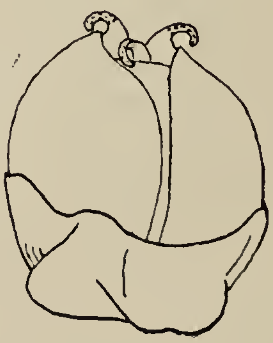
Attached to the Government Botanic Gardens, Saharanpur, Northern India, is a date plantation in which different varieties of date palms, imported from various sources, are under cultivation. Among these occurs a single plant to which the description given by Kearney would apply if the plant were seen in fruit only. Unfortunately the source and history of the plants there growing is not now traceable and it is impossible, therefore, to say whence this particular plant originally came. The attached figures are of different flowers all taken from this single plant. It will be seen that the change does not consist strictly in the substitution of a monoecious for a dioecious habit, but that a whole series of intermediate and hermaphrodite flowers are produced. The exact development of these has not been traced, but it is probable that the few fruits which reach maturity are derived from those female flowers in which the stamens have completely aborted. The condition of the hermaphrodite, intermediate between those of the diclinous, flowers is not confined to the stamens and pistil; a correlated change in the form of the perianth segments also occurs. This is shown in Fig. 4. Here the segment opposite the single developed stamen retains the character of the male flower, the remaining two segments having a form approximating to that characteristic of the female flower.


1


2


3


4


5

LABORATORY NOTE.

A METHOD OF STAINING CYANOPHYCEÆ.

By R. C. McLean.

THE mystery which for long enwrapped the nuclear apparatus of the Cyanophyceæ was due, in no small measure, to the technical difficulties involved in obtaining well stained preparations of the filaments for observation. The massive coat of mucilage which encloses many colonial species, and the sheathing cuticle of others absorb stain so readily and retain it so tenaciously that all details are obscured. Even in species where these natural obstructions are not present the minute size of the filaments render the best regressive methods, even the extremely precise Ferric-Hæmatoxylin, very difficult and tedious to carry out successfully.

Some years ago the present writer made experiments with a view to finding a simple direct acting stain, suitable for the demonstration of the Cyanophycean cell-structure. The result was that a method was found which gives excellent results with great ease. This method was partly original and partly an elaboration of one of the methods used by F. G. Kohl in his study "Uber die Org. und Phys. der Cyanophyceenzelle" (Jena, 1903).

The presence and nature of the primitive form of nuclear apparatus found in these Algæ have already been the subjects of several fine researches, but a great deal regarding their behaviour still remains to be cleared up.

For this reason, and also because it would be desirable, where possible, to introduce these structures into courses on general Cytology, it seems worth while to draw attention to an easy method of preparation. The genus *Oscillatoria*, and in particular the species *O. limosa*, is perhaps the most favourable subject, and occurs constantly in aquarium jars; but practically any of the filamentous forms, especially those with broad cells, are suitable, although the form of the "central body" is not identical in all.

Make up the following stain[1]:—

Rectified Methylene Blue 1 : 5000 aq. dest.
Bismarck Brown 1 : 5000 aq. dest.

Equal quantities. The latter solution is made up by taking of the ordinary 1% solution in 70% alcohol 1 c.c., and adding 50 c.cs. of distilled water.

---

[1] "Rectified" Methylene Blue is that prepared specially for *intra vitam* staining. It may be obtained from any of the agents of Grübler & Co., and is preferable to the ordinary compound for the above purpose.

Place a few c.cs. in a corked tube. Into this stain drop masses of the fresh, living filaments, drained as far as possible of their superfluous water. Leave them in for three days—a somewhat longer immersion does no harm—and then remove and wash in distilled water. Soak for two to three minutes in either 5% Sulphuric acid or 5% Potash Solution, to dissolve the "meta-chromatic granules," which also take the stain, and re-wash in distilled water. Mount in a drop of the highly refractive medium made by dissolving in a saturated solution of Pot. Iodide, as much Mercuric Iodide as it will take up. This medium has a Refractive Index approximating to that of flint glass, and is useful for many purposes, as no dehydration is necessary, while the full aperture of immersion lenses may be brought to bear upon objects mounted in it.

This gives very fine, although ephemeral results. The "central body" stains dark blue, the peripheral protoplasm yellow. The preparations will not last more than twenty-four hours, but this is long enough for demonstration or drawing purposes.

If permanency is an object the preparation must be brought rapidly up from water to 70% alcohol and then dehydrated by means of aniline, cleared in cedar (*not* clove) oil and mounted in xylol-balsam or dammar. The results however are not as brilliant as by the first method.

THE
NEW PHYTOLOGIST.

VOL. XIII, NO. 3. MARCH, 1914.
[PUBLISHED MARCH 31ST, 1914.]

VARIABILITY IN *STELLARIA GRAMINEA*.

BY A. S. HORNE, B.SC., F.G.S., F.L.S.

[WITH TWO FIGURES IN THE TEXT.]

THIS paper is concerned chiefly with variability in the flower of *Stellaria graminea* studied in Surrey and mainly within the precincts of the Royal Horticultural Society's Gardens, at Wisley; and, by the kindness of Dr. C. E. Moss, in the Fen near Abbot's Repton, in Huntingdonshire.

Stellaria graminea, at Wisley, inhabits the grassy verge of the common, frequently reaching a height of two feet or more amongst grass and gorse; other plants, in more open situations, are of shorter stature. The plant flourishes ideally in an uncultivated field within the Gardens, where thousands of the shorter plants grow amongst the herbage and taller ones climb and cling to the outskirts of the clumps of broom. The sub-soil of the field is of sand resembling that of the common hard by; the drainage is therefore good and water does not accumulate during any part of the year, to render the ground swampy. *S. Dilleniana* Mönch (= *S. palustris* Retzius=*S. glauca* Withering) is entirely absent from this locality. In the Fen, however, both *S. graminea* and *S. Dilleniana* occur and occasionally grow in close proximity to one another. *S. graminea* inhabits all the approaches to the fen proper and the narrow footways that penetrate the tall fen-grasses (*Arundo* and *Calamagrostis*). *S. Dilleniana* inhabits the true fen—not extending into the outskirts—and may be found on the banks that confine the dank water-ways choked with various Potamogetons and other water-weeds, or under the shade of the fen-grasses.

My attention was at first attracted by the fact that the flowers in some of the tufts at Wisley possessed a large corolla whilst, in other tufts, a smaller corolla was present. In order to determine whether this difference in size of the corolla was due to local soil-differences, plants of each kind, labelled B and A respectively were chosen, removed from the soil, and after the roots had been well washed, potted in a soil compost consisting of a mixture of sand, leaf-mould and loam. All the flowers of approximately the same age in each plant were measured before removal from the soil—in the case of the corolla, the diameter in millimetres when outspread and the width of the petal-lobe at its widest part. The average dimensions on June 6th, 1912, were as follows:—form B, corolla diameter 14 to 15 mm.: width of petal-lobe 1 to 1·5 mm.; form A, average corolla diameter, 8 to 9 mm.; width of petal-lobe, ·8 to 1 mm. The plants were then placed in the greenhouse adjoining the laboratory, where they soon recovered from the effects of transplanting. A photograph of specimens of the A and B forms, after their recovery, is reproduced in Fig. 1.

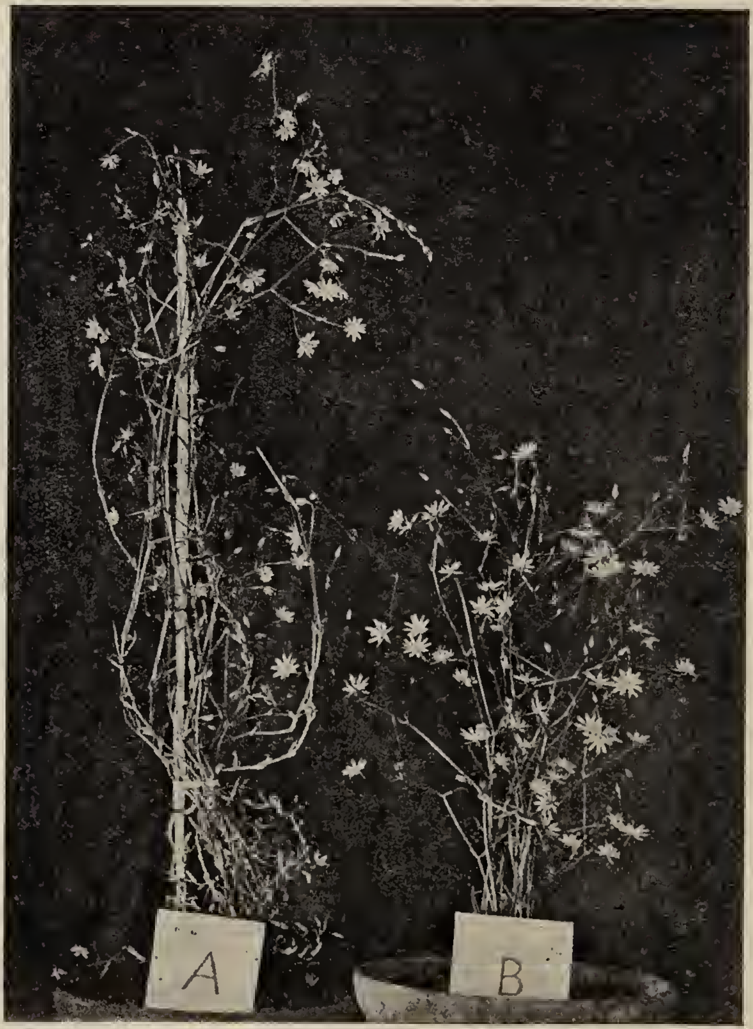


Fig. 1. Photographs of the A and B forms of *Stellaria graminea*. For description see Text.

The transplanted specimens had been taken, in each case, from a patch of *S. graminea* producing flowers of the same dimensions. These patches were staked so that corolla measurements could be made from time to time and compared with those made in the greenhouse. The flowers produced by the potted plants during the first fortnight after transplanting resembled those produced by the parent plants in the open. After this period the flowers produced by B plants decreased in size until they became smaller than those of the A plants, whilst the flowers produced by the A plants remained unchanged until they ceased to bloom. Thus, on June 25th, the diameter of the corolla, in a plant of form A, measured 9·5 mm.; in plants of form B, 7 to 7·5 mm., 5 to 10 mm. and 6·4 to 7 mm. respectively. The experiment was repeated on July 15th and yielded a similar result after fourteen days. In the meantime, the corolla, of form A, in the field, remained unchanged, measuring 9 mm. in diameter throughout August until it ceased to flower, but in the form B, the diameter measured only 12 mm. on July 29th and 12 to 13 mm. on September 24th. A full list of the measurements in millimetres taken is given below:—

GREENHOUSE.

	A.		B.	
1912.	Corolla Diameter.	Width of Lobe.	Corolla Diameter.	Width of Lobe.
June 6	8 to 9	—	15	—
25	9	—	15	—
July 8	8 to 9	0·8 to 1·0	14 to 15	1·1 to 1·5
11	8 to 9	—	—	—
29	9	—	12	—
Aug.—	9	—	—	—
Sep. 24	—	—	12 to 13	1·2
1913.				
July 31	9·5	1·0	14	1·1

FIELD.

1912.				
June 6	8 to 9	—	15	—
25	8	—	7 to 7·5 6·4 to 7 5 to 10	—
July 11	8	—	—	—
15	—	—	7·5	—

Two points may be noted:—(1) that the corolla of only one form (B) responded to a changed environment and produced very small flowers under the experimental conditions chosen; (2) that the corolla of form B varied in size during the season. It is natural, therefore, from these results, to expect some variability in the size of the corolla of form B, in nature, according to the conditions under which the habitat is placed.

A large number of observations on plants in the field had now been made and the dimensions of the flowers of equal age on each plant carefully recorded. The variability in the different parts of the flower may be described as follows:—

The sepals. These are slightly boat-shaped and of triangular outline, with three veins and a membranous margin. In measuring, each sepal was flattened and the width estimated across the widest portion—care being taken to measure from margin to margin. Each sepal is prolonged into a hair-like extremity so that a slight error is introduced in length measurements where the hair is broken or withered. The sepals do not vary in size to the same extent as the petals and stamens. The dimensions, in the plants studied, vary between 5 × 1·3 mm., 4·5 × 1·8 mm., and 3 × 1 mm. Both long and short sepals may be either wide or narrow, such as 4·5 × 1·8 mm. and 3 × 1·6 mm., or 5 × 1·3 mm. and 3 × 1 mm. Longer and shorter sepals are usually found associated with the larger or smaller corollas in the large and small flowered forms respectively.

The corolla. The petals are divided nearly to the base in all the specimens examined. It was found most convenient to take two measurements: (1) the diameter of the corolla; (2) the width of the petal-lobe. The diameter of the corolla was measured when the petals were outspread in a plane passing through the bases of the styles. This character, choosing flowers of approximately equal age, in each case, varied between 15 and 5 mm.; thus, the corollas in one individual measured 14 to 15 mm.; another, 12 to 13 mm.; another, 7 to 8 mm. in diameter, and so on. The width of the petal-lobe was measured in its widest portion. This character sometimes varies in the same flower, but in most plants it is more uniform. It varies from 2 to ·6 mm.; measuring, in one individual, 0·8 to 1 mm.; another, 1 to 1·2 mm.; another, 1·4 mm.; another, 1·8 mm., and so on.

The flowers, of course, present different appearances in the field according to the dimensions of the corolla, but these appearances are also partly influenced by the *shape* of the petals. Thus the corollas, in individuals where the petal-lobes are equi-distant from one another, are ten-rayed; but in individuals where the edges of the neighbouring lobes of adjacent petals touch one another or overlap, the "star" is five-rayed.

The correlation between the diameter of the corolla and the width of its segments is displayed diagrammatically in Fig. 2, where the corolla measurements for a large number of plants are recorded. The letters W and H signify Wisley and Huntingdonshire plants respectively. The horizontal column indicates the width of the

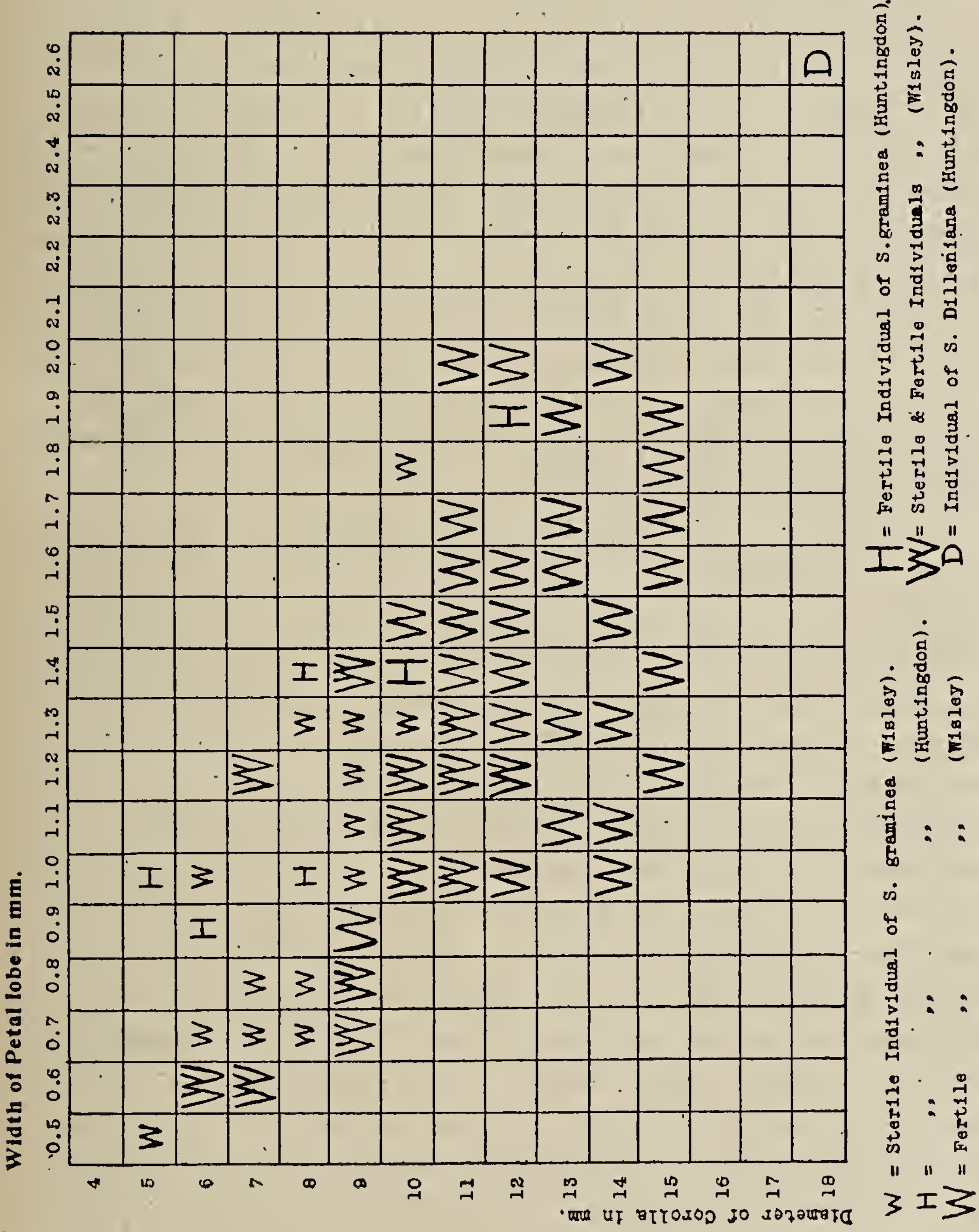


FIG. 2. Diagram to show correlation between stamens and corolla characters in *Stellaria*. For further description see Text.
"Corolla-lobe" should be "petal-lobe" as in Text.

petal-lobe; and the vertical the diameter of the corolla in millimetres. Thus the first W to the left, in the top horizontal column, indicates that a plant bearing flowers with corolla-diameter 5 mm. and width of petal-lobe 0·5 mm. exists at Wisley. It is clear from the diagram that there are large corollas with narrow (cor.-diam. 14 mm., pet.-lobe 1 mm.) or wide (cor.-diam. 14 mm., pet.-lobe 2 mm.) segments; small corollas with narrow (cor.-diam. 7 mm., pet.-lobe 0·6 mm.) or wide (cor.-diam. 8 mm., pet.-lobe 1·4 mm.) segments; and corollas of intermediate kinds. It is also evident that the corollas of smallest diameter possess the narrowest petal-segments (cor.-diam. 5 mm., pet.-lobe 0·5 to 1 mm.).

Stamens. The stamens exhibit puzzling variability. It seemed possible at first to arrange the plants in two sections—one, in which the stamens are of equal size, and equal to or exceeding the sepals, and, but perhaps with rare exceptions, fertile; the other with stamens arranged in two whorls and shorter than the sepals. In the second group the stamens varied in size in different plants. They were all less than one-third of the length of the sepals in some individuals; in others, the stamens of one whorl were one-third and those of the second whorl one-half the sepal-length; in others, one whorl was less than one-third and the second greater than two-thirds of the sepal-length, and so on. The stamens, in this section, proved almost invariably sterile.

A number of individuals were subsequently found with characters that seemed to pertain to both sections, for the flowers on the same plant were not all alike with regard to their stamens. I found flowers with all the stamens short and flowers with stamens of unequal height, varying between the shortest and longest type in the same inflorescence. The inflorescence of another individual possessed two flowers having ten stamens of equal height (largest type) and, on another branch, one flower with four long stamens and six sterile short ones—the latter in two series. The anthers of the long fertile stamens are of a reddish colour before dehiscence but the colour changes to dark-brown after the pollen is shed. The anthers of the shortest sterile stamens are of a pale yellowish colour and wither without becoming red; those of the longer, sterile, but better developed stamens, may redden but do not shed pollen. Among the flowers of the intermediate series, the long stamens closely resemble those of fertile flowers, but they very frequently remain red *after* the styles have developed and do not shed pollen or, if at all, very rarely.

An attempt is made to display the correlation between the stamens and corolla characters in the diagram (Fig. 2) and in order that the representation may not be too complicated, the individuals are scheduled as either fertile or male-sterile—the former are represented by a large W; the latter by a small w. The male-steriles will include a certain number of individuals belonging to the intermediate series. The latter do not, as a rule, possess either the largest or smallest of corollas and on this account will be located toward the middle of the diagram. It will be ascertained from the diagram constructed, by the way, from data yielded by observing some thousands of individuals) that hermaphrodites with a smaller corolla-diameter than 9 mm., and male-steriles with a larger corolla-diameter than 11 mm. are rarely found. Hence the flowers with the largest and smallest corollas are usually hermaphrodite and male-sterile respectively. Flowers with a corolla of medium size may be either hermaphrodite or male-sterile, and hence include individuals of all three series described above. Hermaphrodite and male-sterile individuals with the same corolla dimensions are indicated by placing both a large and a small W in the same square.

The ovary. When the anthers are ripe the styles are quite short, during the period of dehiscence, the latter roll inward presenting a crosier-like appearance, finally, after the pollen is shed, they unroll and spread outwards. The styles when outspread, in the fertile flowers, scarcely exceed the stamens, but they are much longer in the sterile flowers. Both hermaphrodite and male-sterile individuals set good seed.

Comparison with *S. DILLENIANA*.

I have not yet had an opportunity of making a thorough comparison of the flowers of the forms of *S. graminea* with those of the forms of *S. Dilleniana*. In connection with *Stellaria Dilleniana* and its variations, cf. Moss in New Phyt., December, 1912, Dr. Moss informs me that he has found at least four forms of *S. Dilleniana* in the fen :—(1) with large flowers and glaucous leaves; (2) small flowers and glaucous leaves; (3) large flowers and green leaves; (4) small flowers and green leaves. The glaucous form (the old *Stellaria glauca*) and the green form were pointed out to me by Mr. Adamson in July, and I measured the flowers of plants of each kind. The measurements are as follows :—

GLAUCOUS FORM.

	Corolla Diameter.	Petal Lobe.	Sepal Length.	Sepal Width.	Stamens.
1	22	4 to 2·5	8	2·7	=sepals.
2	22	3	7·5	2·5	=sepals.

GREEN FORM.

1	18	2·6	8	2·3	=sepals.
2	20	2·5	7	2·5	=sepals.

It will be noted that both the calyx and corolla in these plants of *S. Dilleniana* are larger than those of the largest flowers of *S. graminea* described here. One individual of the former species is represented in the diagram by the letter D, for comparison with *S. graminea.*

Variation in the flower, in *S. graminea*, is mentioned by Koch[1] in his Synopsis Fl. Germ. et Helvet. in the following words:—[*Stellaria graminea*] "occurrit floribus minoribus et duplo majoribus quæ varietates, observante Schumelius, sexum polygamo-dioïcum indicant: conf. Fl. Sil. i, 417." Two forms of *Stellaria graminea* recorded by Joh. Lange[2] in Haandbog i den Danske Flora, in 1851, appear to agree very closely with the Wisley forms, referred to here as B and A respectively. These are *grandiflora* Petermann, stated to be of male sex, with corolla twice as long as the calyx, and stamens shorter than the petals; and *parviflora* (female) with corolla shorter than the calyx, short and sterile stamens, and style longer than the corolla. These forms are recorded in Gürke's[3] Plantæ Europaeæ but not in Flore de France by Rouy et Foucaud[4] where no reference is made to a male-sterile form. Babington[5] appears to have been the first, in this country, to note variability in the sexual parts of the flower, but it has been suggested to me by Dr. Moss that he was probably indebted to Koch for his first knowledge on the subject. A letter from Babington to Charles Darwin, dated June 6th, 1864, contains the following passage:—"The plants

[1] Koch. Syn. Fl. Germ. et. Helvet. (1837), p. 119.

[2] J. Lange. Haandbog i den Danske Flora (1851), p. 273.

[3] M. Gürke. Plantæ Europaeæ, Tom. II (1897), p. 208.

[4] Rouy et Foucaud. Flore de France, III (1896), p. 234.

[5] C. C. Babington. Memorials, Journals and Botanical Correspondence 1897).

producing different kinds of flowers grew at Sandgate, Kent. The words in my 'Manual,' p. 54, are 'shorter or longer petals accompany an imperfection of the stamens or germen,' but the question has to be re-examined." Two forms—hermaphrodite and female—sent to shew the dimorphism that exists in this species, are commented upon by C. E. Britton[1] in the Report issued by the Botanical Exchange Club for 1908. Brief reference to the variability in *Stellaria graminea* is made in the recent Floras of Cornwall[2] and Bristol.[3]

SUMMARY.

My own observations may be summarized as follows:—

1. Observations made on plants of *Stellaria graminea* growing in a natural Surrey habitat shew that the corollas borne by hermaphrodite individuals during the flowering period varied in size, whereas the corollas produced by male-sterile individuals did not vary in this manner.

2. The corollas formed by hermaphrodite individuals after transference to a different and artificial environment diminished in size whilst those formed by male-sterile individuals under similar conditions exhibited no change.

3. Individuals of all intermediate grades exist in nature with respect to the following characters—long and short petals, wide and narrow petal-lobes, long and short stamens and fertile and sterile stamens.

4. Femaleness is usually associated with corollas ranging from a small to medium size, never with corollas of the largest size, whilst hermaphroditism is usually associated with corollas ranging from a medium to a large size.

5. An intermediate series of individuals exists with flowers which possess some stamens resembling those of hermaphrodite individuals and others which resemble those of male-sterile individuals. Individuals of this series possess a corolla of medium size.

6. From 4 and 5 it is clear that individuals with a corolla of medium size may be either hermaphrodite or male sterile or belong to the intermediate series.

Now a reasonable working hypothesis may be advanced to explain these phenomena. It is possible to sort out from the plexus forms which are definitely male-sterile and hermaphrodite respectively. Individuals of both kinds it will be remembered, set good seed and hence have probably been pollinated. The hermaphrodite individuals cross-pollinate among themselves since the flowers cannot, of course, receive pollen from male-steriles. The male-steriles, on the other hand, if pollinated, receive pollen from hermaphrodite individuals and hence the conditions obtain for Mendelian hybridization. These plants might produce apogamous offspring as in the male-sterile hybrid Œnotheras described by Gates[1]; but in Œnothera the apogamously produced forms appear to be of rare occurrence.

---

[1] C. E. Britton. Rept. Bot. Exchange Club (1908), p. 364.

[2] F. Hamilton Davey. Flora of Cornwall (1909), p. 74.

[3] J. W. White. Bristol Flora (1912), p. 193.

De Vries[2] in the cross *O. lata* (female) × *O. Lamarckiana* (hermaphrodite) found hermaphroditism dominant and obtained segregation into *lata* and *Lamarckiana* forms in the F_2 generation, but Gates,[3] later, did not obtain complete segregation of the parenta characters in this cross. Salaman,[4] on the other hand, finds male-sterility in Potato a dominant character. The cross Record (female) × Flourball (hermaphrodite) produced all sterile plants in F_1, and in F_2, forms with pollen present and pollen absent. It is noteworthy that the forms possessing pollen can be arranged in classes according to their richness or poorness in pollen—the quality of the recessive parent being not fully reproduced. Two plants of the F_1 generation obtained from the cross Congo (female) × Flourball (hermaphrodite) were selfed and forty-four plants were obtained. Of these, three with normal anthers contained no pollen; four, a little; two, medium quantities and thirty-five abundant pollen. Since different results have been obtained by different investigators working with different genera, it is unwise to predict the result of the cross female × hermaphrodite in the case of *S. graminea*. The individuals of the intermediate series referred to above, however, may prove to be hybrid forms obtained in the F_2 generation and I am arranging to test the matter experimentally.

The experiments described in this paper have been carried out with the kind assistance of Mr. C. C. Titchmarsh of the R.H.S. School of Horticulture.

---

[1] R. R. Gates. Science, N.S. XXX, No. 776, p. 691 (1909).

[2] H. de Vries. Die Mutationstheorie, Vol. I, p. 168 (1901-1903).

[3] R. R. Gates. "Pollen Development in Hybrids of *Œnothera lata* × *O. Lamarckiana.*" Bot. Gaz., 43, p. 83 (1907).

[4] Redcliffe N. Salaman. "Male Sterility in Potatoes, a dominant Mendelian Character," Journ. Linn, Soc. Bot., XXXIX, p. 301 (1910).

INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION (I.P.E.) IN AMERICA, 1913. III.

(*continued from p. 41*).

THE DESERTS OF THE GREAT BASIN.

ON the morning of August 23rd the members of the International party awoke to find themselves travelling through the alkali deserts of the basin of the Green River, in the State of Utah. These deserts extend for thousands of square miles within the area of the Great Basin, centering round Great Salt Lake, and in alternation with the sage-brush deserts cover practically the whole of the enormous arid region between the Rocky Mountains and the Sierra Nevada. The dominant plant over wide stretches is the shrubby greasewood (*Sarcobatus vermiculatus*) a shrub about three or four feet high with bright green succulent leaves. The greasewood association alternates with the grey-leaved sage-brush (*Artemisia tridentata*) the most characteristic plant of the whole arid region alluded to. Behind the stretches of level desert rose striking flat-topped hills edged with vertical cliffs running down into fans of talus. For the most part these hills appeared quite bare of vegetation, but on some of the higher ones dark shrubs appeared, probably *Juniperus Utahensis.* By the side of the railroad track were *Salsola, Chrysothamnus, Cleome lutea, Helianthus, Gutierrezia,* the yellowness of nearly all the flowers visible being a striking feature. *Melilotus alba,* species of *Salix,* and even *Typha* were seen in places along the track. Where the land was irrigable good crops of oats and alfalfa were being raised, and trees, particularly cottonwoods and Lombardy poplars, were flourishing.

The Wasatch Mountains forming a westward extension of the Rockies and separating the basin of the Green River (a tributary of the Colorado River) from the Great Salt Lake basin were soon entered and the deserts temporarily left behind.

The picturesque Price River canyon, lined with *Populus angustifolia, Salix* spp. and *Acer Negundo* along the streamside, was entered at Castlegate, and scrub and coniferous trees, reminiscent of the Rocky Mountains, were soon encountered. In the lateral gullies was scrub of *Quercus, Rhus, Cercocarpus* and *Fendlera : Pinus ponderosa* appeared on the slopes, and soon afterwards Douglas fir. The drier slopes nearer the line were still covered with sage-brush, here growing more densely. On the further side of the Wasatch

Mountains drier conditions again prevailed and the Pignon-Juniper formation (*Pinus edulis* and *Juniperus Utahensis*) was met with.

The country traversed by the railroad between this point and Salt Lake City is practically all irrigated and highly cultivated, with orchards, alfalfa, corn, etc. Of planted trees *Salix babylonica*, Lombardy and other poplars and *Catalpa* are conspicuous.

The party received a warm welcome at Salt Lake City, where they were entertained to lunch—prefaced by a specially excellent cocktail—at the Commercial Club, the remainder of the day being spent in sight-seeing, including a trip to Saltair Beach, where several members of the party enjoyed the peculiar experience of bathing in the Lake. An area of salt flat with *Distichlis*, *Allenrolfea*, *Salicornia*, etc., was visited on the way.

On Sunday, August 24th, the day was spent in the Tooele valley to the south of Great Salt Lake, the scene, during 1912, of very careful vegetation and habitat analysis by Messrs. Kearney, Briggs and Shantz, of the United States Department of Agriculture. The train was taken to Tooele, and the party drove from that point to Grantsville close to the Lake, where the Union Pacific railroad was taken back to Salt Lake City. Stops were made at frequent intervals and the various plant-associations visited.

Tooele valley is about sixteen miles long, thirteen miles broad at its upper (southern) end and seventeen miles broad at its northern (lower) end where it becomes continuous with the flat southern shore of the lake. The difference of level between Tooele (at the upper) and Grantsville (at the lower end) is about 680 feet. The mountains rise steeply from the sides of the valley, whose floor is covered by a great depth of alluvial deposits largely of Eocene age. The area was afterwards covered by the waters of "Lake Bonneville" which occupied the whole area in Pleistocene times. No permanent streams now reach the valley proper. During the Lake Bonneville period the waters of the Salt Lake basin reached a maximum of 1000 feet above the present level of Great Salt Lake, and this level is marked by conspicuous beach lines on the surrounding mountains.

The present climate is semi-arid, evaporation greatly exceeding the average rainfall of about sixteen inches per annum, and Great Salt Lake is still shrinking fairly rapidly.

The natural vegetation of the valley shows a very striking zonation of associations roughly parallel with the lake shore. These are in general correlated with the total salt-content of the soil, but no correlation was found with the chemical composition of the soil solution. The soils of the Tooele valley are all more or less saline, with the exception of that of the sage-brush (uppermost) association, and that of the sand hills mixed association (which was not visited by the party).

The following associations were distinguished by the Department of Agriculture workers and demonstrated to the international party.

(1). Sage-brush association dominated by *Artemisia tridentata.* This occupies the highest alluvial fans and benches nearest the mountains and has the most sandy soil (with the exception of the sand hills—not considered here), the lowest moisture equivalent and the lowest salt-content (·03 to ·07%) of any of the associations. At the time of this visit the association was very poor floristically, the dominant sage-brush being practically pure, with societies of *Gutierrezia* and some *Agropyron spicatum.* There is, however, a distinct vernal flora coinciding with the rains of May (the wettest month, averaging 2·4 inches), and containing *Phlox*, *Castilleia*, *Delphinium*, etc. During the summer the surface foot of soil is dry, the water-content sinking below the wilting point, and the next few feet of soil are similarly dry in late summer. *Juniperus Utahensis* occurs in this association near the mountains.

(2). *Kochia vestita* association. This occupies the next zone and is again nearly a pure association of the dominant. The soil is more clayey, the surface foot to which the roots of *Kochia* are confined being leached of salt (surface foot ·12%, fourth foot 1·11%). The moisture equivalent is a good deal higher than in the sage-brush association, the summer water-content being still below the wilting point.

(3). Shadscale association, dominated by *Atriplex confertifolia* occupying the next lower zone does not differ markedly in physical factors from the previous association.

(4). Greasewood-shadscale association dominated by a mixture of *Atriplex confertifolia* and *Sarcobatus vermiculatus.* The moisture equivalent of this association does not differ much from those of the two last, but the average summer water-content is much higher, and except in the surface foot available water is present during the summer. The salt-content is decidedly higher at all depths, though the leaching effect is still observable in the surface foot. This is apparently the factor which brings in the greasewood, a pronounced halophyte. It is said that the availability of the water-content is

[1] The quantity of water, expressed as a percentage of the dry weight of the soil, retained by the soil against a centrifugal force 1,000 times the force of gravity.

not decreased by the high salt-content; and this is in line with most of the modern work on the physiology of halophytes. *Suæda Moquinii*, another marked halophyte, forms societies in this association.

The secondary species are much the same throughout this series of associations—*Chrysothamnus graveolens* and *Gutierrezia Sarothræ* being the most conspicuous species.

(5). We now come to the salt flat association, dominated by *Allenrolfea occidentalis* (a *Salicornia*-like plant with alternate instead of opposite leaves) or alternatively by the grass *Distichlis spicata* or by *Salicornia Utahensis*. In this association the high salt-content (1 to 1·25%) which is present at the greater depths under associations (2) to (4), extends to the surface foot of soil, the water table is much higher, and there is available water at all depths during the whole year. The association extends to the edge of the lake and consists of extensive mud flats covered in summer with a glistening white crust of salt and broken by low ridges and hummocks. The vegetation is of an open type.

There is another association strongly irrigated by springs, etc., which has been called the marsh mixed association. It is less saline than (4) and (5) and contains a more varied flora including *Sporobolus airoides*, *Juncus balticus*, etc. This is dependent on local irrigation and does not form part of the series described above.

There is probably no case in which the physical factors determining the occurrence of a series of associations have been worked out so satisfactorily and completely as in these associations of Tooele valley, which appear to be typical of a large part of the Salt Lake basin.

Where the land is irrigated good crops are raised, and the Lombardy poplars are specially fine.

ARID REGIONS OF THE SNAKE AND COLUMBIA RIVER BASINS.

About midnight the party left Salt Lake City by the Oregon Short Line, and the next two days were spent mainly in the train, traversing the states of Idaho, north-eastern Oregon and Washington. During the whole of August 25th the train traversed sage-brush desert in the Snake River valley (Idaho) from Pocatello (Idaho) to Huntingdon just over the Oregon State line, which was reached in the evening. The monotonous grey sage-brush association with occasional patches of grass (*Agropyron*, etc.) and here and there the bright yellow-flowered *Chrysothamnus*, was broken only by occasional cultivation, the isolated farms invariably sheltered by belts of the ubiquitous Lombardy poplars. During the night we traversed the Blue Mountains, and in the morning were in the Columbia River basin. Entering the state of Washington at Wallawalla we traversed during the whole day that remarkable region of eastern Washington known as the Great Plain of the Columbia River. This immense region, covered by a great basaltic lava-sheet weathering into a fine dust-like soil, is a very important agricultural area in spite of its low rainfall (fourteen to twenty inches). Typical dry farming with wheat and summer fallow alternating is here practised. The hills as far as the eye could reach were entirely under the plough with scarcely a trace of natural vegetation visible, the only variation in the uniform grey tone occurring at the lines between the yellower wheat stubble and the browner fallow. For hour after hour we travelled through this perfectly uniform landscape. In the valleys on the irrigated land were fruit orchards and the usual rows of Lombardy poplars. The roads were mere dust tracks except where they had been "paved" with wheat straw. Such fragments of vegetation as could be seen was either dry "prairie" of *Agropyron spicatum* or occasional stretches of sage-brush now much burned up by the great heat.

In the evening the party arrived (very late) at the important and flourishing city of Spokane, where the members were received by a committee of citizens and driven in automobiles through the brightly lighted streets to the famous Davenport's Café—said to be the best restaurant in all the north-west—entertained to a peculiarly excellent supper, perhaps the best meal partaken of throughout the trip, and, after speeches, were driven back to the station. Short as was our stay in Spokane it formed a most charming and exceedingly welcome interlude in the long railroad journey.

The early morning of August 27th saw our arrival at North Yakima in the centre of a district which has recently undergone rapid agricultural development. The sage-brush land of which the floor of the Yakima River valley consists, makes, when irrigated, a very favourable soil both for wheat and orchard cultivation. The party were again received by a local committee and taken in automobiles through the beautifully kept apple and peach orchards, where we inspected the process of packing the fruit and stowing it in ventilated and refrigerated fruit cars drawn up on branch railroad tracks immediately outside the packing sheds. The city of North Yakima showed very clearly the evidences of recent great prosperity. The neat little houses with beautifully kept vividly green grass and gay flower beds, contrasted strikingly with vacant lots of waste land not yet taken up, and great stretches of well-tended orchard. Unfortunately there was no time to see the primitive sage-brush land, of which none is now left in the immediate neighbourhood of the town. The peaches were ripe and were much appreciated by the members of the party.

NORTH-WESTERN CONIFEROUS FORESTS.

North Yakima was left about midday, and during the journey to Tacoma (160 miles) the Cascade Mountains were crossed, an important range running north and south parallel to, and about 100 miles from, the Pacific coast, extending from British Columbia southward for several hundred miles to the southern limit of Oregon, where they become continuous with the Sierra Nevada. The Cascade range has several isolated peaks rising above 14,000 feet, of which the chief is Mount Rainier, whose snow-covered summit was seen to the south from the train. The ridge was crossed through Stampede Tunnel two miles long at 2,810 feet, the overlying pass having an elevation of 3,980 feet. The Cascades form a very important barrier between the western coastal region of high rainfall (131 inches is reached in some places) and the arid region to the east through which we had been travelling and in which the rainfall is generally considerably below 20 inches and may be as low as 7 inches in the year. This striking climatic difference is of course reflected in the vegetation. As the ridge is ascended from the east the sage-brush vegetation gradually gives place to *Pinus ponderosa*, which increases in numbers and is itself replaced by Douglas fir (*Pseudotsuga mucronata*) associated with *Thuja gigantea (plicata)* and *Tsuga heterophylla*.

Thus we entered the wet north-western conifer region of which the Douglas fir is the typical dominant. Its growth here is immensely more luxuriant than in the Rockies, and it is associated with other species, both of trees and of ground-vegetation, though some of the Rocky Mountains species are still present. Much of this area has been cut over and burned, and is now a wilderness of charred stumps and weeds which have replaced the once magnificent forest. The forests on the watershed are, however, National Forests, in the hands of the Federal Government, and these are leased to contractors who fell the timber under the direction of the Government foresters, provision being made for proper regeneration. The forest lands in the hands of private lumber companies are completely cleared of timber and are often subsequently burned over more than once, effectually preventing the return of the forest trees. The land is then abandoned till it can be sold for farming, at a very low price, *e.g.*, $15 an acre, but the very heavy cost—at least $100 an acre—of clearing the ground of tree-stumps imposes a charge so heavy that farming is often unremunerative.

The night of August 27th was spent at the large city of Tacoma on the southern extremity of Puget Sound, and on the following day the party travelled in the morning to Kapowsin where they spent part of the day at a lumber camp as the guests of the Tacoma and Saint Paul Lumber Company. The land belonging to this company is situated on the foothills of the Cascades and once bore splendid Douglas forest, most of which has now been removed. Portions of as yet untouched forest were visited by the party, and presented a magnificent specimen of virgin mesophytic forest.

The forest was dominated by *Pseudotsuga mucronata*, in close stand, often making up 90% of the forest, the average height of the trees being 200 feet. Mature trees are 300 to 400 years old, and 6 or 8 feet in diameter at the base. Some giants measure as much as 14 feet across and these may approach an age of 1,000 years, though in general trees of over 500 years are rare. Associated with *Pseudotsuga* are *Tsuga heterophylla* and *Thuja gigantea*, and also *Abies grandis* and *A. nobilis*. The coastal species *Picea sitchensis* is rare. Of small trees or shrubs, *Acer macrophyllum* is common; *A. circinatum* and *A. glabrum* also occur; also *Rhamnus Purshiana*. The red-berried huckleberry, *Vaccinium parvifolium*, four or five feet high, occurs, and the Devil's Club, *Echinopanax (Fatsia) horrida* with its tall stout prickly stems and large palmately lobed leaves is a great feature under the forest shade. Of ferns, *Polystichum munitum*, the "Christmas fern," *Adiantum pedatum*, var. *alenticum* and *Blechnum boreale* are common, and the conspicuous lichen often covers the dead branches of the trees *Equisetum sylvaticum*, *Oxalis* sp. (close to *O. Acetosella*) *Tiarella*, and various other shade-forms are found on the ground.

After lumbering various quickly spreading plants at first colonise the soil—conspicuous among which are *Epilobium angustifolium* and *Anaphalis margaritacea*. A species of *Senecio* is also in evidence. *Pteridium aquilinum*, which is absent from the heaviest forest, comes slowly in, and shrub-genera such as *Alnus*, *Salix*, *Corylus*, *Sambucus*, also increase. The conifers come back pretty quickly in normal regeneration, but, as has been said, these areas are so often repeatedly burned over that the young trees are destroyed and all chance of regeneration vanishes. The derelict land left after these repeated burnings is covered with great stretches of weeds, and presents an indescribable appearance of waste, ruin and desolation, which considerably depressed various European members of the party.

On leaving Kapowsin the train was taken up country as far as Ashford, through the splendid canyon of the Nisqually River, whose sides are still largely covered with fine Douglas forest. Much of this country too has been devastated by the lumbermen. We were told that even so recently as 1900 the ride from near Tacoma up to Mount Rainier was through untouched Douglas forest all the way, with but a few insignificant clearings at intervals.

From Ashford the automobile journey up to the National Park Inn at Longmire's Springs is partly through the Rainier National Forest and mostly within the Mount Rainier National Park. In a National Forest lumbering is carried on by private individuals or companies under the direction of the Government foresters, but a National Park is a real nature-reserve in which nothing is allowed to be touched except by special permit. The great National Parks of the west, of which the Yellowstone and the Yosemite are the most widely known examples, form one of the possessions of which the United States may most justly be proud. Three of them were visited by the international party in the course of their travels.

The lower part of the Mount Rainier Park is covered with typical and often very fine Douglas forest, though scarcely so fine as the Douglas forest of the lower hills near the coast, which, being in private hands, has already almost disappeared. The dominant Douglas fir is often very pure, and the vegetation is of the same general type as that seen in the unfelled forest near the lumber camp already described. The trees, considering their immense size, grow pretty close together and the shade is very deep. Huge fallen logs lie prostrate in all directions, so that rapid progress through the forest is difficult. *Tsuga heterophylla*, much more tolerant of shade than *Pseudotsuga* and so regenerating freely in the Douglas woods, *Thuja plicata*, also tolerant of shade, *Abies grandis* and *Picea sitchensis*, enter into the composition of the forest in various proportions. At about 300 years of age, according to Mr. Munger, a Government forester who was with the party in the Rainier forests, Douglas fir begins to suffer, and as the tree does not reproduce itself under its own shade it gradually gives place to *Tsuga* and *Thuja*. On this view a *Tsuga-Thuja* forest is the ultimate type in this area, and there would be no pure Douglas stands if it were not for the forest fires which allow the succession to begin over again. The causes of the occupation of so much of the country by Douglas forest would then be the long duration of the Douglas stage and the frequency of fires. This view is not, however, shared by all authorities well acquainted with the country. *Pseudotsuga* comes in very early on land once burned over.

Arbutus Menziesii, whose headquarters are in the sugar-pine *(Pinus Lambertiana)* area on the Californian Sierra, extends up the the coast through Oregon as far as Vancouver Island, where it occurs mainly on warm dry slopes. A few trees occur so far inland as this Rainier area. The distribution of this species furnishes an interesting parallel with that of *Arbutus Unedo* in Europe, whose headquarters are in a warm dry region, but which extends up the west coast so far north as south-west Ireland. In both cases the mild winters of these northern coast-regions are no doubt the factor which makes such a distribution possible.

The shrubby undergrowth consists of *Acer circinatum, A. glabrum, Ribes bracteosum, Rubus spectabilis, Vaccinium parvifolium, Berberis nervosa, Gaultheria Shallon,* etc. These and the ground-flora form, however, a very open vegetation on account of the dense shade. In clearings or on areas recently burned over *Epilobium angustifolium* and *Pteridium aquilinum* are very conspicuous, exactly as they are in similar situations in north-west Europe. In the deep shade of the forest itself the herbaceous vegetation is rather sparse and consists of such species as the tall Devil's Club (*Echinopanax horrida*) which is abundant and conspicuous, *Cornus canadensis* (a northern herbaceous species much like the European *Cornus suecica*), *Maianthemum bifolium* var. *dilatatum, Smilacina* sp., *Tiarella,* etc., with abundant ferns—*Blechnum boreale, Polystichum munitum, Phegopteris Dryopteris, Athyrium cyclosorum.* These together with many of the angiospermous herbs frequently grow on the immense fallen logs met with in every direction and covered with thick carpets and cushions of mosses and liverworts.

Dicotyledonous trees are practically absent from the Douglas forests, but often form a belt along the stream-sides. *Alnus oregana, Acer macrophyllum* and *A. circinatum* are the chief species in such situations, with *Populus trichocarpa* (closely allied to *P. balsamifera*), and *Fraxinus oregana.*

The Douglas woods extend up to about 2,000 or 2,500 feet, and as one ascends are gradually replaced by mixed woods of *Abies amabilis, A. nobilis, Tsuga heterophylla, Pinus monticola, Chamæcyparis nootkatensis* (the Alaska cedar). The ground-vegetation contains many of the same species as in the lower forest, with such forms as *Linnæa borealis*, *Clintonia*, *Pterospora andromedea*, etc.

Mount Rainier.

On the morning of August 29th, after a night spent at Longmire's Springs, the party made their way up the upper Nisqually valley through the coniferous woods just mentioned, past the snout of the Nisqually Glacier, and spent two nights at the "Camp of the Clouds" situated in the sub-alpine parkland at 5,500 feet, above the limit of continuous forest. August 30th was spent on the slopes of Mount Rainier, and on August 31st the party returned to Tacoma. The sub-alpine meadowland round the "Camp of the Clouds" contains a great wealth of beautiful herbaceous forms, including *Valeriana sitchensis*, *Castilleia oreophila*, *Pulsatilla occidentalis*, *Gnaphalium lanceolatum*, *Eriogynia pectinata*, *Hieracium gracile*, *Polygonum bistortoides*, *Lupinus Lyellii*. The trees, which are scattered in clumps and lines, are mainly *Abies lasiocarpa*, a tall narrow pyramidal tree, which, as "Krüppelholz," forms the actual tree-limit at 6,800 feet. Mount Rainier, a great rounded volcanic cone 14,530 feet high and with the upper 5,000 feet or so covered with snow, towers magnificently above these slopes, which are composed of talus and rock and possess many beautiful alpines, such as *Lupinus Lyellii*, *Saxifraga Tolmeana*, *Antennaria*, *Phlox Douglasii*, etc.

"Oak Openings."

On September 1st the "oak-openings" at Spanaway Lake in the neighbourhood of Tacoma were visited. These are patches of prairie in the middle of rather open woodland of Douglas fir with *Fraxinus oregana* (shore of the lake), *Alnus oregana*, *Acer circinatum*, *Corylus californica*, *Salix* sp. and *Pteridium* abundant on the ground. *Quercus Garryana* was scattered along the edge of the prairie, and the grassland itself was largely composed of a species of *Festuca*, with *Leontodon* sp. abundant, and locally *Pteridium*. *Pseudotsuga* was clearly slowly invading the prairie, many seedlings in all stages of growth occurring on the edge of the grassland. Whether the latter was primitive and the observed invasion part of a secular process not yet complete, or whether these local prairies owe their origin to fires occurring in the thin woodland developed on the rather poor gravel and humus soil, as is perhaps more likely, is a question which remains obscure.

Some members of the party visited the *Nereocystis* beds in Puget Sound.

(*to be continued*).

NOTES ON RECENT LITERATURE.

A NEW FERN-LIKE STEM, DESCRIBED BY COUNT SOLMS-LAUBACH.

LAST year Count Solms-Laubach[1] published a very interesting account of a fossilised fragment of stem from Brazil. The fossil is evidently part of a Fern-like plant and appears to come from the same geological horizon as the Lepidodendra, Cordaiteæ and Psaronieæ that have been recorded by Derby from that part of Brazil. Count Solms gives to this new stem, from near Tieté, the name of *Tietea singularis.*

The fossil consists of a fragment of a stem, at the periphery of which are the remains of two leaf-bases. The innermost part of the stem preserved—which may or may not represent the central region of the original stem—consists of a number of solenosteles scattered irregularly in an originally homogeneous ground-tissue. Usually these steles form closed rings, but the ring may be broken in one or more places, so that the place of a solenostele may be taken by a number of small strands more or less circular in transverse section; in other cases the steles may bear irregular projections or branches. The xylem of these steles consists of the polygonal, scalariform tracheides so common in the Ferns; in each strand the xylem is broken up into nests of tracheides separated by rays or bands of parenchyma. There are also parenchymatous intrusions or splits. These intrusions are described as being widest at the periphery of the xylem, narrowing as they pass inwards and occasionally becoming branched; they consist of rather small-celled parenchyma in connection with the surrounding phloëm-parenchyma. Though the position of the protoxylem could not be certainly determined, owing to poor preservation, Count Solms thought that, if present, it was probably in contact with these intrusions.

The leaf-traces are large; they originate by the division and branching of a number of peripheral steles of the stem. These leaf-trace-bundles at first form a transverse series, but, apparently somewhat irregular divisions soon give rise to three rows of small bundles, somewhat circular in transverse section, lying one outside the other. The two inner rows supplied the petiole; the outermost row, distinguished by the markedly larger diameters of its steles, passes out first and enters a sort of sheath ("Decke"), external to the trace. After entering the sheath the number of the bundles diminishes considerably; a little higher up the sheath itself forks into two divergent projections or lobes, and here the bundles undergo a further reduction in number, and the resulting bundles appear to be more freely branched or subject to greater fusion. It is from the bundles of these lobe-like projections that the vascular systems of the adventitious roots arise.

---

[1] "*Tietea singularis.* Ein neuer fossiler Pteridineen stamm aus Brasilien." Zeitschrift für Botanik, Bd. 5, 1913, pp. 673-700, with Pls. VI and VII.

Finally the outer part of the ground-tissue of this curious fossil was traversed by numerous roots, running parallel with the stem.

It would, of course, be rash to draw any final conclusions as to the affinities of *Tietea* from the material at present available. The fossil consists of a short fragment of the stem, incomplete transversely; the leaves, after they become free from the stem, and the fructifications are completely unknown. In the absence of the latter organs it is impossible to be sure whether we are dealing with a true Fern or a Pteridosperm. Nevertheless the vascular structure of the plant is highly peculiar and after reading Count Solms' detailed analysis of it it is impossible not to be struck by points suggesting comparison with certain better known groups.

The most obvious comparison is with the Psaronieæ, and it is on this comparison that Count Solms dwells, though he concludes by stating that for the present "we must resign ourselves to leaving the question of the relationship of *Tietea* to the Psaronieæ *in suspenso*" (l.c., p. 700).

Taking first the points of resemblance, one of the most curious is the similarity of the root-traversed peripheral tissues of *Tietia* and those of the Psaronieæ. The paucity of the material limited the number of sections of those parts that could be obtained; but while admitting that more light might be thrown on this matter Count Solms remarks that the structure of this tissue seems to point to the conclusion that it had a similar origin to that of the root-traversed-tissue of the Psaronieæ. His own recently published investigations on the so-called radiciferous cortex of *Psaronius* seem to show that this tissue is mainly cauline in origin, but that a certain amount of the peripheral part arose from the roots themselves.[1] It would surely be a significant fact if this morphologically peculiar tissue should obtain also in *Tietea*. Count Solms further points out that the structure of the xylem is not essentially different in *Tietea* and *Psaronius*, though in latter the parenchymatous intrusions found in *Tietea* "become unusually unimportant ('ausserordentlich zurücktreten') in *Psaronius* and are practically confined to the occurrence of small nests of parenchyma in the tracheal tissue." But there are also very striking differences. One of the most obvious of these is that in *Tietea* the trace originates as a number of distinct bundles, while in *Psaronius* it is a single wide band. Further the presence of the sheath that ends in lobe-like prolongations is peculiar to *Tietea*. Neither of these differences, however, appears of such importance as the following facts: (1) *Psaronius* is definitely polycyclic, while *Tietea*, though highly polystelic, shows no sign of polycycly; (2) the reparatory strands, which in *Psaronius* take part in the formation of the trace and give rise to the adventitious roots, are absent in *Tietea*, where the latter function is assumed by the bundles of the lobe-like prolongations, the absence of reparatory strands seems to be correlated with the absence of polycycly; (3) the leaf-trace of *Tietea* is not only multi-fascicular at its origin, but the numerous bundles composing it soon arrange themselves in more than one series, even excluding those destined to the sheath; (4) the plate- or band-like steles of *Tietea* appear very different from the solenostelic, usually annular steles, of *Tietea*.

[1] Solms-Laubach, H. Graf zu. "Der tiefschwarze Psaronius Haidingeri von Manebach in Thüringen." Zeitschrift für Botanik, Bd. 3, Heft. 11, 1911.

In regard to the last difference Count Solms remarks that M. Zeiller has figured for *Psaronius brasiliensis* and *P. infarctus* fusions of steles leading to a ring-like band (" ringförmige Schleife ") or to a ring with but a small break. If we imagine this process to be extended to all the steles of *Psaronius*—a conception that Count Solms regards as offering no great difficulty—we should arrive at an image bearing a far-reaching similarity to the structure of our *Tietea*. Specimens intermediate in this character between *Tietea* and typical Psaronieæ do seem to exist, for Count Solms possesses an undescribed *Psaronius* from Brazil in which ring-like closed steles, or open branched ones such as are characteristic of *Tietea*, occur in many places. It is true that these steles occur only at the periphery, the central part being occupied by small crowded strands, of the type usual in *Psaronius* and strongly reminiscent of *P. infarctus*. If the comparison with *Tietea* were to be carried through we should have, Count Solms says, to assume the whole of the centre of the stem of *Tietea* to be missing, an assumption leading to an improbable, though not impossible, enlargement of the circumference of the stem. It is worth noting, however, that in Zeiller's figures, as reproduced by Seward,[1] some of the more internal steles of *P. infarctus* itself are branched. Owing to the fragmentary preservation of the fossil Count Solms was unfortunately not in a position to study the traces, which would have shown whether the specimen was a *Psaronius* or a *Tietea*. It is to be regretted too that Count Solms' photograph of this fossil (Pl. VII, Fig. 7), rather less than life size, does not clearly show how far the polycycly of *Psaronius* was retained in this *Tietea*-like stem.

While these facts afford some support for the view that the nearest affinities of *Tietea* may be with *Psaronius*—and this is all that Count Solms suggests—the marked polycycly of most of the latter seems to me a very serious difficulty. The origin of the polycyclic condition from the monocyclic has been so frequently traced of late years that it seems legitimate to conclude that it is always a derivative condition ; if so, *Tietea* may be derived from a more primitive monocyclic *Psaronius*. Dr. Scott mentions a *Psaronius* that, in part at least of its stem, seems to be not only monocyclic but monostelic.[2] This species seems, too, to have been solenostelic ; but this does not seem to me to make it any easier to see in it an anatomical resemblance to a precursor of *Tietea*. For though the evolution of so-called " polystely " from solenostely has been repeatedly traced and seems to be generally brought about by the overlapping of leaf-gaps, yet there seems to be no case known of the development in the ontogeny of several solenosteles from a single one, except in the case of such polycyclic solenostely as that of *Matonia*. Nor do I see how the numerous solenosteles of *Tietea* could arise from a single solenostele by any of the established tendencies leading to stelar complication.

In the elaboration of its leaf-trace *Tietea* has followed a course to some extent parallel to that of the Marattiaceæ. Not only are the traces of both multifascicular from their origin, but in both the bundles are arranged in several series. In a large leaf of *Angiopteris*

---

[1] Seward, A. C. "Fossil Plants. Vol. II." Cambridge, 1910, p. 416, Fig. 296A.

[2] Scott, D. H. " Studies in Fossil Botany." Ed. 2, vol. I, 1908, pp. 301-2.

evecta Mm. Bertrand and Cornaille distinguished 113 separate bundles arranged in four series.[1] In *Tietea* the trace has not so far been found to consist of more than three series, and though the exact number of bundles is not mentioned by Count Solms it was evidently much inferior to the number recorded for the petiole of *Angiopteris*. But it is probable that in the free *Tietea*-leaf the number of series of bundles may have equalled or exceeded that in *Angiopteris*, for at the point of entry into the stem the Marattiaceous leaf-trace is much simplified. Finally, in the shape of the individual bundles of the trace and in the details of its development, notably in the relation of the external series of bundles entering the sheath, and the Marattiaceous stipular bundles to the rest of the trace, the two types are markedly different. These differences and the apparent impossibility of deriving the stelar system of *Tietea* from a Marattiaceous type, seem to preclude the possibility of a close affinity between *Tietea* and the Marattiaceæ.

[1] Bertrand, C. E., and Cornaille, F. "Etude sur quelques caractéristiques de la structure des filicinées actuelles. I. La masse libéroligneuse élémentaire des filicineés actuelles et ses principaux mode d'agencement dans la fronde." Travaux et mémoires de l'Université de Lille, Tome X, No. 29, 1902, p. 167.

ISABEL M. P. BROWNE.

CHONDRIOSOMES (MITOCHONDRIA) AND THEIR SIGNIFICANCE.

By F. Cavers.

Introduction.—Animal Chondriosomes.

A CONSIDERABLE literature, including a large proportion of controversy, has grown during the last few years around certain cell constituents, first observed in animals and later in plants and variously termed "chondriosomes," "mitochondria," "chondriomiten," "chondriokonten," etc.

The name applied originally (in 1886) by La Valette St. George who appears to have been the first to describe, or at any rate to name, these bodies was "cytomikrosomen." This writer found in the male cells of certain insects small highly refractive bodies which showed dense *intra vitam* staining with Dahlia and were either isolated or arranged in filaments. Henking (1891) and Toyama (1894) described similar bodies in their observations on spermatogenesis in insects. Apparently, however, the first detailed investigation of these bodies was made by two other zoologists, Benda and Meves, each of whom published a long series of papers on the subject—Benda's papers ranging from 1897 to 1902 and those by

Meves from 1897 to 1911. Both writers showed that bodies like those of those described by the earlier observers occurred not only in the male cells of insects but in those of a large number of animals both vertebrate and invertebrate.

Benda termed these bodies mitochondria (μίτος thread, χόνδριον grain) from their tendency to occur in rows or filaments, and suggested that they constitute a new cell-organ probably characteristic of active cells, since he found that they occurred not only in the developing sexual organs but also in various kinds of somatic cells (young muscle fibres, leucocytes, etc.)—in fact, he believed that they might be found, at any rate in traces, in all cells rich in cytoplasm. Benda's special service was the working out of special methods of fixation and staining[1] whereby the presence of mitochondria might be demonstrated not only with special certainty and beauty in sperm-cells but in different somatic cells of a large number of animals. Meves suggested that Benda's "mitochondria" were identical with La Valette St. George's "cytomicrosomes," and he studied especially the behaviour of these bodies during mitosis of the spermatocytes of various animals.

Benda had, in 1899, put forward the hypothesis that they represent a motor-organ of the cell, because in various animals he found that the greater part of the middle piece of the spermatozoon was developed from the mitochondria which at first are scattered in the spermatogenous cells. The behaviour of the chondriosomes in spermatogenesis differs somewhat in different animals. In many insects and worms they are scattered in the cytoplasm of the young spermatogenous cells as fine grains, but during the divisions of these cells they become elongated and divide by median constriction; when the final division has taken place, the chondriosomes of the spermatid become aggregated into a rounded mass ("Nebenkern"); during the differentiation of the spermatozoon this mass divides into two portions which become elongated with the growth of the tail part of the spermatozoon, one end of each filament remaining close to the nucleus, and again become granular; finally the granules fuse together to form homogeneous filaments which by lateral fusion constitute a closed sheath around the axial thread of the tail. In mammals, etc., the chondriosomes do not show a "Nebenkern" stage but simply form a granular sheath around the axial thread of the middle portion of the sperm.

Meves (1899) claimed that Benda's motor-organ view is untenable, for he found that when the terminal portion of a living salamander sperm, which is free from mitochondria, is cut off, this portion remains capable of movement. However, Meves entirely agreed with a second suggestion made by Benda in his 1903 paper—namely, that in any case the portion of the sperm containing the mitochondria undoubtedly enters the egg at fertilisation, that the female sexual cells also contain mitochondria, that these bodies occur in large numbers in the blastomeres of the young embryo, and that they may play an important part in the conveyance of hereditary characters. Meves was led by cytological observations on various vertebrate embryos to support the hypothesis that the mitochondria function in this manner; he found that these bodies occur in all the cells of the young embryo, but only rarely appear as grains, being usually more or less elongated and mostly coiled smooth filaments of uniform thickness throughout their length. Meves termed these homogeneous filaments "chondriokonten," in order to distinguish them from filaments ("chondromiten") consisting of rows of mitochondria. Both types of structure—mitochondria and chondriokonten—Meves comprised under the collective term "chondriosomes," but the majority of later writers have continued to use "chondriosomes" and "mitochondria" as synonymous terms.

---

[1] See Lee, A. B. "The Microtomist's Vade-mecum," ed. 6, 1905, p. 223.

Meves repeated and elaborated his views in his later papers, suggesting that the chondriosomes form the material ("Anlage-substanz") for the various processes of differentiation which the tissues undergo in the course of development from the fertilised egg. He expressly states that he does not regard these bodies as *the* inheritance carriers to the exclusion of the nucleus, but he considers that while the nuclear qualities are conveyed by the chromosomes, those of the cytoplasm are carried by the chondriosomes. He claimed (1910) to have observed the mitochondria of the sperm of *Ascaris* fuse with those of the egg. In a more recent paper (1911) he points out that the chondriosome theory harmonises the views of Flemming (1882) and of Altmann (1890) regarding cytoplasmic structure—the former considering it as filamentous and the latter as granular[1]—and suggests the general term "plastosomen" for these bodies, terming them "plastokonten" if filamentous, "plastochondrien" if granular: "Die Chondriokonten oder Plastokonten sind mit den Fila Flemming's von 1882, die Mitochondrien oder Plastochondrien with den Körnern Altmann's identisch." Perroncito (1910, 1911), however, considered that the mitochondria are homologous neither with Altmann's "granula" nor with Flemming's "Filarwatte," and suggested that a distinction should be drawn between Meves's "chondriokonten" (to which Perroncito limits the term chondriosomes) and Benda's mitochondria; the first point is of course a purely controversial one, and as regards the second it may be stated that observers of both animal and plant chondriosomes have traced every transition stage between homogeneous filaments, moniliform filaments and isolated mitochondria.

Various later writers—Duesberg, Van der Stricht, Giglio-Tos, Granata, Lams, Regaud, Fauré-Fremiet, Hoven and others—have confirmed the observations of Benda and Meves, and some have also supported the view that the chondriosomes play an important part as carriers of cytoplasm in the fertilisation process. Against those writers who have combatted his views and have upheld the theory that the nucleus alone is concerned in fertilisation and inheritance, Meves (1908) argues very reasonably that on his view a single minute mitochondrium might suffice to convey the characters of the paternal cytoplasm into the egg.

---

[1] This somewhat bald statement may be amplified by remarking that Flemming rejected the view regarding the constitution of cytoplasm advocated by Frohmann—that there is a reticulum embedded in a homogeneous ground substance—and, denying the existence of a reticulum, laid stress on the presence of a fibrillar structure, the fibrils or filar elements being threads embedded in a more fluid inter-filar mass; while Altmann insisted on the importance of certain granules ("bioblasts") which form essential constituents of the cytoplasm, as distinguished from others which have been formed by the cytoplasm and are more or less accidental inclusions in it.

ANIMAL CHROMIDIA.

In 1909, Goldschmidt, who had previously (1904) described for various tissues in *Ascaris* what he termed the "chromidial apparatus," sought to bring his observations on chromidial bodies into line with the work of Benda and Meves. The term chromidia was introduced by Hertwig (1902)[1] who found that in *Actinosphærium Eichhornii* the protoplasm contained, in addition to the numerous nuclei, a large number of scattered and extremely small bodies which he likened to minute Amœbæ and which were stained with carmine in exactly the same manner as the nuclei. These bodies increased in number when the organism was either overfed or on the other hand starved and they then often became aggregated into clumps that were eventually expelled from the cell. According to Hertwig these chromidia arise from the chromatin of the nucleus and are in fact simply extruded portions of this substance. Goldschmidt found that chromidia occurred in the cells of the most diverse animal tissues but particularly in young or actively growing and functioning cells, were frequently arranged in filaments and in other ways, and were not only deeply staining bodies but often actually took up chromatin stains more intensely than the nucleus itself. He extended Hertwig's term chromidia to cover "alle jene Zellstrukturen wie Mitochondrien, Pseudochromosomen, Trophospongien, Dotterkern, Nebenkern, apparato reticulare, als ein und dieselbe Einrichtung lebhaft funktionierender Zellen." For the various forms of this "chromidial apparatus" he suggested the terms chromidia, chromidial filaments, chromidial bodies, chromidial net, etc., and he came to the conclusion that all active metabolic and other changes in the animal cell are inaugurated by the extrusion of nuclear chromatin into the cytoplasm, where—either directly through chemical change or indirectly by providing energy set free by its decomposition—it assists in bringing about various metabolic and formative processes.

GENERAL CHARACTERS OF ANIMAL CHONDRIOSOMES AND CHROMIDIA.

To summarise the foregoing condensed and very incomplete, though perhaps for our purpose adequate, account of the zoological literature of our subject, it has been claimed that the granular or filamentous bodies referred to (and variously termed granula, bioblasts, mitochondria, chondriomiten, chondriosomes, chondriomes, chromidia, chromidial apparatus, sphæroblasts, histomeres, trophochromidia, somatochromidia, granulochromidia, plastosomes, plastokonts, plastochondria, etc., etc.) are all essentially homologous structures; that they occur in the cytoplasm of probably all animal cells; that they play a specially important rôle in spermatogenesis; that they provide material and energy for the multifarious processes of metabolism, growth and differentiation of animal cells; that they may be either on the one hand special cytoplasmic structures or on the other hand chromatin extrusions from the nucleus; that they act as the carriers of the hereditary qualities of the cytoplasm just as the chromosomes carry those of the nucleus, and that they thus play an important part in fertilisation and heredity. It is obvious that much further work is necessary before definite conclusions can be drawn as to the real nature of these various bodies and before one can really say what they are and what they do.

---

[1] Chromidia appear to have been noted first by Schaudinn in Foraminifera, but their significance was first fully recognised and generalised by Hertwig. Until the appearance of Goldschmidt's paper (1904) they appear to have been observed only in the Protozoa, and are described and figured in various works dealing with this group—*e.g.*, Lankester's "Treatise on Zoology," Part I, Fasc. 1 and 2; "Cambridge Natural History," vol. 1. They occur in many Sarcodina and some Sporozoa, and are described as being given off as small fragments from the nucleus, or the latter may be resolved into chromidia, and by their growth and coalescence they may form new nuclei. In a recent paper on the chromidia of the Protozoa, Swarczewsky (1912) draws a sharp distinction between the "gametochromidia" of the parasitic Protozoa which provide material for the formation of sexual nuclei, and chromidia which do not so function. On the other hand, Fauré-Fremiet (1910) has described the occurrence in many Protozoa and Flagellata of bodies which do not arise from the nucleus and which agree with the chondriosomes of higher animals in form and general behaviour, dividing simultaneously with the division of the organism itself; in various Ciliata the chrondriosomes are arranged close to the periphery of the body and are evidently related in some way to the cilia.

Apart from Meves's far-reaching hypothesis as to the rôle played by the chondriosomes in inheritance and the demonstration that they take a large share in the formation of spermatozoa, the chief functions assigned to animal chondriosomes are those of motor-organs and of nutritive bodies. For the former view stress has been laid on their occurrence in muscle-fibres, in the stalk of *Vorticella* and the tentacle of *Noctiluca*, etc.; while their frequent presence in glands lends support to the latter view. According to Regaud the chondriosomes form the mother-substance of the secretion-grains produced in glandular cells. Hoven found that in pancreas cells homogeneous filamentous chondriosomes were present before secretion began, and these later were transformed into chains of mitochondria which soon became isolated and grew into secretion-granules.

Little is known concerning the chemical composition of animal chondriosomes. Regaud found that they consist of a protoplasmic ground-mass together with a substance which is soluble in alcohol but becomes insoluble on treatment with chromic acid; according to Fauré-Fremiet and others they contain a fatty acid adsorbed by an albuminoid ground-substance.

As regards the origin of the chondriosomes, all that can be said at present is that most workers on animal chondriosomes consider that they are *sui generis* structures ("omne mitochondrium e mitochondrio"), that they should be sharply distinguished from true chromidia arising by nuclear extrusion, and that most of the so-called chromidia are probably to be included under chondriosomes—the exact converse of Goldschmidt's theory.

DISCOVERY OF CHONDRIOSOMES IN PLANTS.

The bodies which we may here for convenience lump together as chondriosomes had become familiar in zoological literature long before they were described as occurring in plants. Their occurrence in vegetable cells was first described by Meves in 1904. He found them in the tapetum cells of young anthers of *Nymphæa alba*, fixed with Flemming's fluid and stained on the slide with Meves' iron hæmatoxylin method.[1] He describes the tapetum cells as containing numerous small but unequal-sized vacuoles, one or two nuclei, and in addition a number of fairly thick, elongated and irregularly coiled filaments which stained black with iron hæmatoxylin. In most of the cells these threads are in one or two places aggregated to form dense knots. He says "Diese Fäden können nun auf Grund ihres Aussehens und ihrer Färbbarkeit nicht wohl etwas anderes sein als die von tierischen Zellen bekannten Chondriomiten."

---

[1] As described in Strasburger's "Botanisches Praktikum," Aufl. 4, p. 70.

Meves's observations on plant chondriosomes were later confirmed and extended by a considerable number of other workers to whose papers reference will be made presently. It may be noted here, however, that some of the earliest of these adopted Goldschmidt's "chromidial apparatus" view. Beer (1905) observed in the tapetum cells of Onagraceæ bodies consisting of chromidial substance, similar in form to those found by Meves in *Nymphæa*, and stated that they were invariably of nuclear origin, arising either from the chromatin and nucleolar substance or from the peripheral portions of degenerating nuclei. Tischler (1906) described for the tapetum cells of *Ribes intermedium* rods and filaments consisting of rows of deeply staining grains, which he considered had migrated from the nucleus into the cytoplasm, so that while confirming Meves's discovery of chondriosomes in plants he agreed with Goldschmidt in regarding them as to nuclear origin. Von Derschau (1907, 1909) found similar bodies in the tapetum and spore mother cells of various Monocotyledons as well as in vegetative tissues of *Vicia faba*, and claimed to have observed in some cases portions of the chromatin actually escaping from the nucleus, causing protuberances of the nuclear membrane and then passing into the cytoplasm outside—part of the chromidial grains remained close to the nucleus while the rest though moving to some distance still remained in organic connexion with it. It should be noted that while Meves observed his "mitochondria" only in tapetum cells with resting nuclei, Tischler and von Derschau observed their "chromidia" in cells with dividing nuclei; von Derschau, for instance, describes them in the prophase division of pollen mother cells and figures the escape of chromidial substance through the nuclear membrane at this stage. It is doubtful whether the structures described by Tischler and von Derschau can have nothing to do with the mitochondria of Benda and Meves, while they also differ in various respects from Goldschmidt's chromidial apparatus. Tischler's work was soon criticised by Duesberg and Hoven (see below), who considered that his view of the nuclear origin of the filaments observed in the tapetum cells of *Ribes* was based upon faulty material or observation; and later Tischler himself in a review (Bot. Centralbl., Bd. 119, 1911, p. 276) of Pensa's work (see below) stated that he had come to the conclusion that he had in fact worked with degenerating tapetum cells and had described phenomena resulting from death of the nucleus and having nothing to do with chromidial bodies found in meristematic or healthy cells, also that he was in agreement with the conclusions meanwhile arrived at by Lundegard (see below).

More recently, Arnoldi and Börnicke (1911) have described chondriosome-like bodies in the jacket-cells around the oosphere of *Dammara*, and in the tapetum cells of the anthers of *Larix*, *Bryonia* and *Cucumis*. In the former case the nucleolus is described as becoming angular and finally indefinite in form and passing into a network at the periphery of the nucleus, while deeply-staining bodies appear in the cytoplasm and evidently represent chromidial substance which has escaped from the nucleus of the jacket-cells and which eventually passes in the form of chromidia or chondriosomes into the oosphere; in the latter case the chondriosome-like bodies appear in the tapetum cells at the tetrad division of the microspore mother-cells and as the tapetum cells break down these bodies pass into the spaces between the microspores. In both cases the chromidial bodies are regarded as being derived from the nucleus and as serving a nutritive function.

Thus, as in the case of animal cells, two distinct kinds of origin have been ascribed to plant chondriosomes—by some they are described as consisting of chromatin extruded from the nucleus, by others as cell-organs *sui generis*—or, to put it in another way, there have been described two kinds of deeply staining chondriosome-like bodies in the cytoplasm. Whether these bodies really belong to two distinct categories, or are all of nuclear origin, or all of non-nuclear origin and in that case always formed by division of pre-existing bodies of the same nature or formed *de novo* by differentiation of the cytoplasm, are questions that at present can hardly be answered but which must await further investigation.

FURTHER WORK ON PLANT CHONDRIOSOMES UP TO 1910.

Before proceeding to consider the important publications of Lundegard, Lewitsky and Pensa which appeared in 1910 and formed the main basis of subsequent work on plant chondriosomes, mention may be made of the work of some other writers who followed Meves and simply confirmed the observation that bodies more or less precisely resembling those described by him occurred in various plant cells. Von Smirnow (1907) described chondriosomes in the cells of *Hyacinthus* roots and in *Pisum* seedlings, in fresh as well as in stained preparations; this writer, though apparently ignorant of the work of Goldschmidt, Beer and Tischler, since he refers only to Meves's 1904 paper on plant chromosomes, considered that the bodies observed by him probably arose from the nucleus, near which they usually occurred, but he makes the guarded statement that despite the apparent identity in form and staining behaviour between animal and plant chondriosomes nothing definite can be said concerning their nature so long as microchemical data are lacking. Duesberg and Hoven (1910), who found in vegetative cells of *Pisum, Phaseolus vulgaris* and *Allium porrum* seedlings and *Tradescantia* leaves, treated according to Benda's method, typical granular and filamentous chondriosomes like those described by Meves, stated emphatically that these bodies did not arise from the nucleus and could not therefore be regarded as consisting of chromidial substance. Nicolosi-Roncati (1910) studied the chondriosomes in the pollen-mother-cells of *Helleborus*, observing isolated and seriate mitochondria and more complex forms arising by fusion of these; he regarded the "mitochondrial apparatus" as having for its rôle the equal distribution of chromidial substance between the two daughter cells. Numerous other papers published since Meves's discovery of plant chondriosomes need not be mentioned here, since they contain nothing of special interest; as in the case of animal chondriosomes, there is fairly general agreement regarding the *sui generis* nature of these bodies, though there also seems little doubt that in some cases nuclear matter is extruded into the cytoplasm in the form of "chromidia." Many earlier observations were also recalled in which various writers had described and figured granular or filamentous bodies in the cytoplasm of vegetable cells which might or might not be regarded as chondriosomes—*e.g.*, the chondriosome-like bodies found by Mikosch (1894) in epidermis and parenchyma cells of *Sedum*, *Sempervivum* and *Malva*, scattered in the cytoplasm or associated with the nucleus and the plastids though apparently quite distinct from either; by Schniewind-Thies (1897) in the septal nectaries of Liliaceæ and Amaryllidaceæ; by Bouin (1898) in the embryo-sac of various Liliaceæ; and so on.

LUNDEGARD'S VIEW OF PLANT CHONDRIOSOMES AS DEFORMED PLASTIDS.

Lundegard (1910) worked with root-tips of *Vicia faba*, fixed with strong Flemming and stained with hæmatoxylin, and in his study of nuclear and cell-division in the apical meristem found that the cells invariably showed chondriosome-like structures in the cytoplasm. He then fixed entire roots before cutting off the root-tip, in order to eliminate changes in the cells attributable to wound reaction; he dipped them for ten to thirty seconds in 1% chromic acid, cut off the tips and placed them in weak Flemming, and stained the sections with iron hæmatoxylin or gentian violet. The same granular, vesicular and especially filamentous bodies were observed in the cytoplasm, chiefly around the nucleus. Next he cut longitudinal sections of living roots, which showed in the dermatogen and periblem numerous leucoplasts, mostly scattered in the cytoplasm but sometimes aggregated around the nucleus; and on adding to the sections various fixatives (strong and weak Flemming, iodine, chromic acid, etc.) found that the leucoplasts almost instantly showed changes in shape and position. These consisted usually in aggregation around the nucleus of previously scattered leucoplasts, but the latter frequently broke up into small portions which formed either scattered aggregates or moniliform filaments; these changes Lundegard compared with the phenomena of systrophe or balling undergone by chromatophores as the result of various stimuli (changes in illumination, etc.) and long ago described by Schimper and others. Various other structures were formed which differed in form according to the fixative and stain employed, and these bore a striking resemblance to the various forms of chondriosomes; moreover, according to the strength of the fixative and the time during which it was allowed to act on the cells, every stage was obtained between normal leucoplasts and the variously deformed and chondriosome-like ones. Lundegard therefore concluded that part at any rate of the structures described as vegetable chondriosomes are simply by the action of fixatives, plastids deformed and in this sense mere artefacts.

DISCOVERY OF THE ORIGIN OF PLASTIDS FROM CHONDRIOSOMES.

Almost simultaneously with this critical work of Lundegard's there appeared in 1910 a paper by Lewitsky and another by Pensa which opened a new chapter in the investigation of plant chondriosomes. Lewitsky (1910) studied various tissues of *Pisum* and *Asparagus*, using various fixatives, and in all cases obtained the same results: the cytoplasm contains filamentous and granular chondriosomes corresponding precisely with those of animal cells; these bodies undergo division; they neither occur within the nucleus nor arise from the latter; in somatic cells of root and stem-tip they are irregularly scattered but during nuclear division tend to collect at the poles of the spindle, whereas in the dividing pollen-mother-cells they form a mantle around the spindle but are absent from the poles. The most remarkable result however was the transformation of the chondriosomes in the root-tip cells into leucoplasts and that of those in the stem-tip into chloroplasts, which Lewitsky claimed to have demonstrated. In this process the chondriosome swells at each end while the middle portion becomes longer and thinner, then the substance of the pyriform or spindle-shaped portions loses its homogeneity and is differentiated into a darkly-staining outer layer and a clear central region, the latter being traversed by fine but sharply defined threads. Meanwhile each end has grown in size and the two young plastids formed by the disappearance of the connecting thread gradually assume the definite characters of leucoplasts or chloroplasts by further growth and division. The quite young cells at the growing-point contained only chondriosomes, but in older cells their number diminished as that of the leucoplasts or chloroplasts increased.

Pensa (1910), who independently came to the same conclusion, at first studied the ovaries of various plants, using both the Benda-Meves method and the reduced-silver methods of Golgi and Cajal, and carefully traced the behaviour of the chondriosomes as well as that of the nuclei in successive stages of development. The chondriosomes appeared as rounded or ovoid grains which were either scattered through the cytoplasm or showed a tendency to aggregation at the periphery of the cell or on the other hand around the nucleus, and which grew in size as the development of the flower-bud proceeded. Frequently, as in *Tulipa*, these bodies had the form of rings or of a network: in other cases they were rod-like or filamentous and either straight or curved in various ways. He concluded that these bodies give rise to chromatophores, and that in fact they represent various stages in the development of leucoplasts and chloroplasts, while at the same time they are morphologically similar to the chondriosomes of animals.[1] Pensa later (1911) admitted that the Benda fixative is not well adapted to the study of this subject since it causes disorganisation of the stroma of the chloroplast and granular deformations of the included starch-grains which then stained deeply with hæmatoxylin. Pensa agreed with Lundegard that certain fixatives (especially those with chromic acid) are unsuitable, but contended that the silver method is free from this objection and that the structures he observed were certainly not artificial. He found that the blackening of the plastids with the silver method depended upon the presence of chlorophyll but not upon that of starch, and that this reaction

[1] "Tutte queste formazioni che ho descritto e che si colorana in nero col metodo dell'argento ridotto e che somigliano, dal punto di vista morphologico, in modo cosi perfetto ai mitocondri delle cellule animali sono intimamente legate alla formazione dei cloroleuciti o corpo clorofilliani, anzi rappresentano le varie fasi di sviluppo dei cloroleuciti stessi. È facile convincersene perchè i cloroleuciti completamente formati si colorano anch'essi in nero o in bruno col metodo indicato e si possono seguire i varii stadii di passagio dalle forme più svariate di granuli, di bastoncini, di filamenti a quelle per le quali è indubbia a nature di cloroplasta."—Pensa (1910), p. 330.

was given when the merest traces of chlorophyll appeared, for instance, when etiolated seedlings were exposed to light for a few hours. Using both the Meves's staining method and the silver method, he traced the formation of chloroplasts from chondriosomes in the young leaves of a considerable number of flowering plants, and fully confirmed Lewitsky's results.

Forenbacher (1911) studied the origin of chloroplasts and leucoplasts in the stem and root of *Tradescantia*, for fixing which he used chiefly a modified form of Benda's fluid consisting of chromic acid and osmic acid, acetic acid being omitted, but also used absolute alcohol which he found to give good results, while in addition to Meves's modification of Heidenhain iron-hæmatoxylin he used the well-known triple stain (safranin, gentian violet, orange). He began with fully developed plastids and proceeded towards the growing meristem, and found every stage between these and the chondriosomes of the young growing cells, the intermediate forms being dumb-bell structures exactly like those described by Lewitsky.

Lewitsky published two further papers in 1912. In the first of these he gives side by side photographs of living cells of *Elodea* and of cells fixed and stained by the Benda-Meves method, to show that the chondriosomes are not in any sense artefacts but can be seen quite clearly in suitable living cells. He then tried various fixative fluids and divides them into two groups—those which give the real structure of the cytoplasm and show the chondriosomes in their natural condition (Benda's fluid, the same minus acetic acid, Altmann's fluid, 0·5% osmic acid, 10% formalin, weak Flemming) and those which give various deformed products and artefacts and are therefore unsuitable for work on chondriosomes (absolute alcohol, Carnoy's acetic alcohol, mixtures containing corrosive sublimate, silver nitrate plus pyrogallic acid, strong Flemming). These various fluids were tried both with microtome sections and with living cells (the axillary scales of *Elodea* were used) examined directly under the microscope. In the second paper Lewitsky points out that many of the methods hitherto used in the study of the development of plastids are quite unsuitable, since they cause deformation of the chondriosomes from which the plastids originate. As in his earlier work he found that the plastids arise as swellings of the ends of filamentous or rodlike chondriosomes, and he gives photographs of the young choroplasts in the "chondriokont stage."

During 1911 and 1912 Guillermond published a series of papers giving the results of an elaborate investigation of chondriosomes with special reference to their function as the forerunners of plastids, and confirmed and greatly extended the work of Lewitsky and Pensa. He used various methods, but chiefly that devised by Regaud for animal chondriosomes. He examined plants belonging to all the main divisions of the vegetable kingdom and found chondriosomes in nearly every case (reference will be made later to his work on chondriosomes in fungi), but his first papers dealt mainly with the behaviour of these bodies in germinating seeds, particularly those of Gramineæ. Here he found that the chondriosomes in the cotyledon mostly remained unchanged, while those in the meristem cells mostly disappeared as plastids were formed at their expense. In the cells at the base of the young leaf these bodies at first lie close to the nucleus as short filaments which during mitosis arrange themselves around the spindle, but in anaphase move towards the poles so that each daughter cell receives an approximately equal number of chondriosomes which then again become arranged around the nucleus in close contact with its membrane. The filaments (chondriokonts) then undergo segmentation so as to form short rods, and as leaf development proceeds these swell up, become ovoid grains, and are eventually transformed into chloroplasts. In his later papers Guillermond found that chondriosomes occur in every cell of a flowering plant, whether vegetative or reproductive, so that they may be traced throughout the life cycle, being invariably formed by division of pre-existing chondriosomes derived in the first instance from the chondriosomes of the parent pollen-tube and oosphere—hence in this respect plant chondriosomes are homologous with those of animals; that they are therefore cytoplasmic structures *sui generis*; and that they may either remain unaltered or may be transformed into leucoplasts or further into chloroplasts—and, conversely, that chromatophores (in flowering plants at any rate) are invariably formed by the growth and modification of chondriosomes. He found that leucoplasts were formed in somewhat different ways in different plants—*e.g.*, as small swellings at various points on a chondriokont (seedling of *Pisum*, *Zea*, *Ricinus*, etc.), as large fusiform bodies arising from an entire chondriokont (*Phajus* tuber), by differentiation of the constituent granules of a chondriomite (*Ranunculus Ficaria* tuber), or by that of isolated mitochondria (potato tuber), and so on. In his work on the buds of adult plants he obtained the same results as in the case of seedlings, the formation of chloroplasts in the stem cortex and in the leaves derived from the meristem of the bud taking place exactly in the same manner as in the plumule of seedlings, while the chondriosomes of the stem stele persisted without change or were transformed into leucoplasts. As in the case of leucoplasts, the mitochondria swell up, the central portion becomes clear and but little stainable as compared with the peripheral portion, and eventually one or several starch grains appear in this central portion.

In the longest of his later papers on this subject (Arch. d'Anat. Microsc., 1912, pp. 309-428) Guillermond summarises the work done by himself and others up to that time on the origin of plastids from chondriosomes, and points out that the morphological criterion —"la différenciation morphologique des mitochondries," that is, the origin of plastids "d'un simple accroissement de volume de ces éléments"—does not afford a sufficiently exact definition of chondriosomes; "comme les mitochondries et les leucoplastes se colorent de la même manière, il est donc extrémement difficile d'établir une distinction entre ces deux formations." Hence he attempts to define and distinguish these bodies on their microchemical characters, and from his results he concludes that while plastids show the same stain reactions as chondriosomes, the latter are usually soluble in alcohol and acetic acid while the former are not. He does not lay much stress upon the results obtained at present but remarks that much further microchemical work is required, and he concludes that "mitochondries et leucoplastes sont donc des formations apparentées qui paraissent constituées d'une substance très voisine."

(*to be continued*).

MARLOTH (R.) THE FLORA OF SOUTH AFRICA.

With synoptical tables of the genera of the higher plants, 180 coloured plates, 100 monochrome plates, and 300 figures in the text. Four Volumes. 4to. Buckram binding.

SUBSCRIPTION PRICE £2. 2*s*. NET EACH VOLUME.

VOL. I NOW READY.

Published by

WILLIAM WESLEY & SON

28 ESSEX STREET, STRAND, LONDON.

REVIEW.

"THE FLORA OF SOUTH AFRICA," BY DR. R. MARLOTH.

THANKS to the munificence of Lady Phillips and to the knowledge and industry of Dr. Marloth, the botanical world is about to be presented with one of the most splendid " Floras " which has ever seen the light, containing 180 coloured and 100 monochrome plates (originals being the work of four ladies and one gentleman), together with 300 figures in the text, of which most of the photographs are by the author, others by Messrs. W. Galpin, J. S. Henkel, P. S. Laney, A. Elliott, E. Dyke, E. J. Steer, I. Miering, J. Belgrove, A. J. Fuller, A. G. Cook, and A. Rogers; some of the sketches, microscopic and otherwise, are by Mr. W. T. Saxton.

The " book is written chiefly for the general reader and the beginner in botanical studies." Only the *first* volume out of four has so far appeared.

Endlicher's grouping of 1840 has been adopted, *viz.*, into Thallophyta (Lower Plants) and Cormophyta (Higher Plants). The latter comprise the Archegoniatæ and Anthophyta. The characteristics of all these groups are briefly described and lucidly figured as in a text-book, and the principal members of each group occurring in South Africa (from Walfisch Bay to mouth of the Limpopo being the northern boundary, Rhodesia being excluded) are described and the vast majority of the natural orders (" families " in this work) are most generously, beautifully and, in most cases, faithfully represented on the coloured plates; but the Mosses, Chenopodiaceæ, Amarantaceæ, Nymphæaceæ, Ceratophylleæ, and one or two lesser orders, are not so favoured, a fact which the reviewer regrets, as far as the Mosses and Water Lilies are concerned. The paintings of the entire plant and of the female inflorescence of *Welwitschia* are, however, very far from doing justice to the beauty, form[1] and actual colouring of these objects as one sees them growing in their natural habitat; but this can hardly be expected, for the paintings were perforce made partly from semi-mummified specimens and partly from the imagination; the colour of the female cones when fresh is really quite different from that given in the sketch by Miss Dixie; on the other hand the male inflorescence is much truer, although one misses the tinge of delicate green in the cones.

Some of the pleasing features of the book are: the very clear type, the citation of popular names of the plants where known, and the keys to the genera given throughout. The author, who has travelled extensively in South Africa, speaks with authoritative first-hand knowledge of the majority of the plants treated of.

For those whom no kind Fate leads into the great flower-paradise of the Land of Sunshine in the far South this great book will come, perhaps, as the next best thing, *i.e.*, if it is accessible, for the price (£2 2s. per volume) must greatly limit its circulation, and one cannot imagine such a work paying its way.

By means of this book, replete with clear descriptions, lavish of beautiful photographs, splendid with paintings of flowers, and (for the student) well-furnished with genera-keys, the wondrous flora of the Cape (using the term in its widest sense) is brought one stage nearer to the stay-at-home botanists of Europe, and in a way which has never been equalled before.

One further point. The reviewer had occasion to mention recently at the Linnean Society that many of the Cape plants in the greenhouses at Kew had grown, owing to the over-moist and under-illuminated conditions, almost out of all recognition to one who knows them in their native haunts; robust plants become drawn, flaggy and often utterly grotesque. Dr. Marloth refers to this same phenomenon in his work: "*Protea cynaroides* was seen by us in flower at Kew in May, 1911, but the shoots were thin and slender, over ten feet high and tied up against a trellis, not stout and robust as on the wild plant." Here, then, we have one more reason for welcoming this unique work; it will help to save home-botanists from the misleading ideas created from the contemplation of cultivated Cape plants in Europe!

[1] The leaf, in the living plant, is not split up into ribbons, as is here portrayed.

W.C.W.

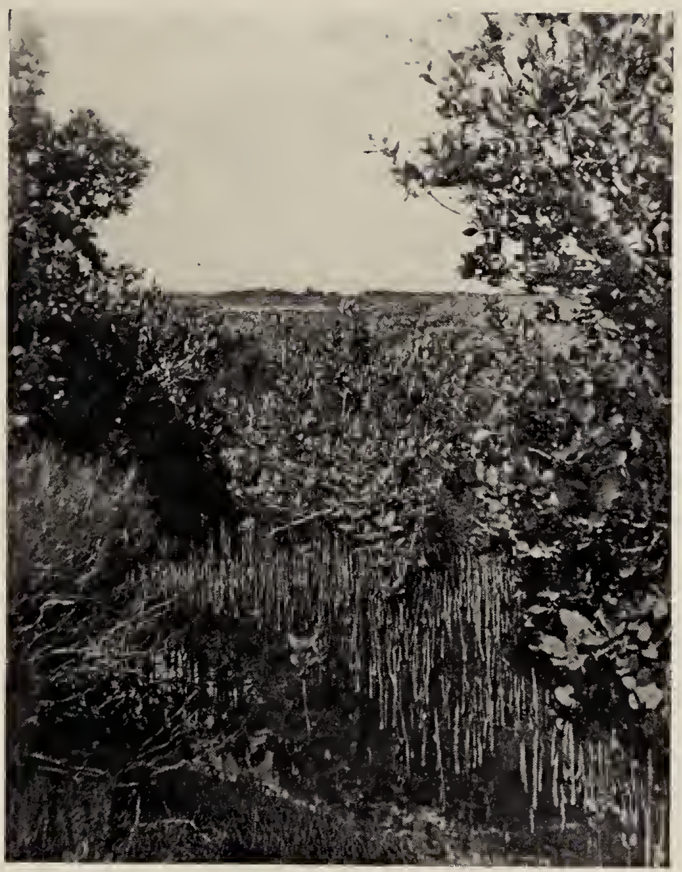


Fig. 1.

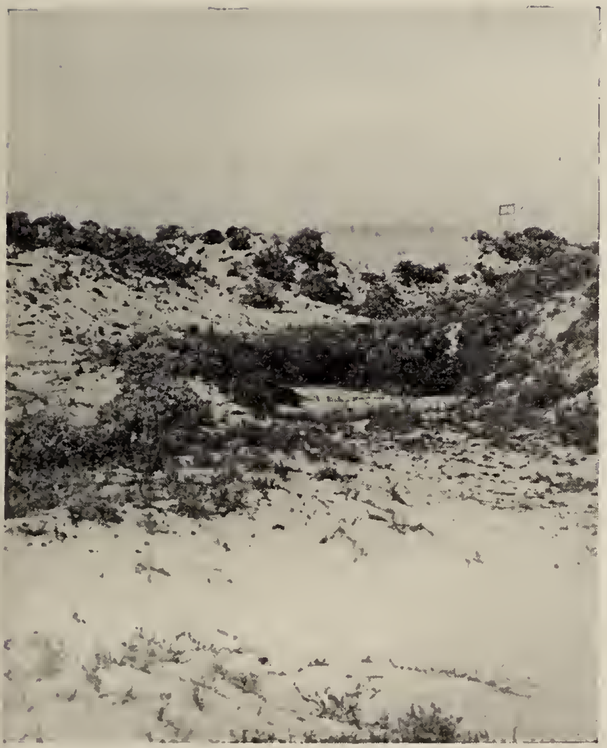


Fig 2.

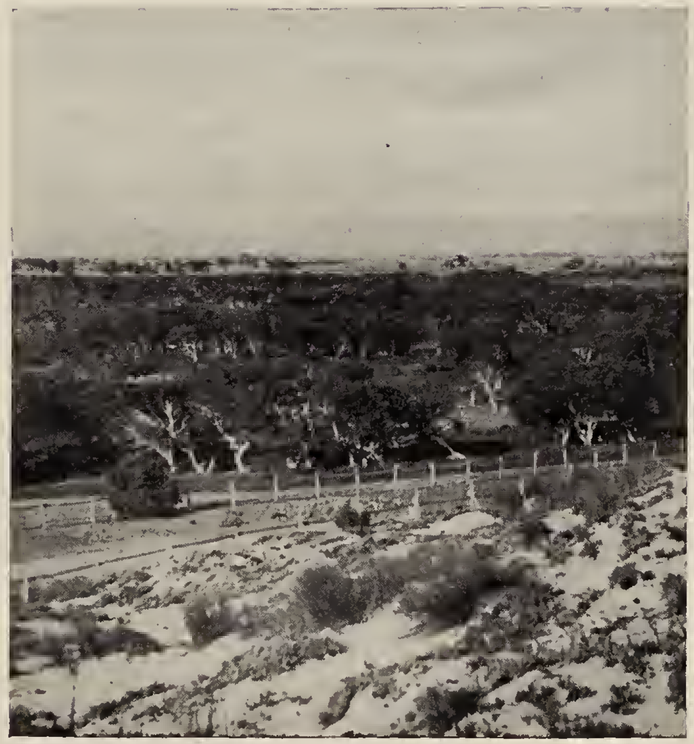


Fig. 3.

OSBORN.—FLORA AROUND ADELAIDE.

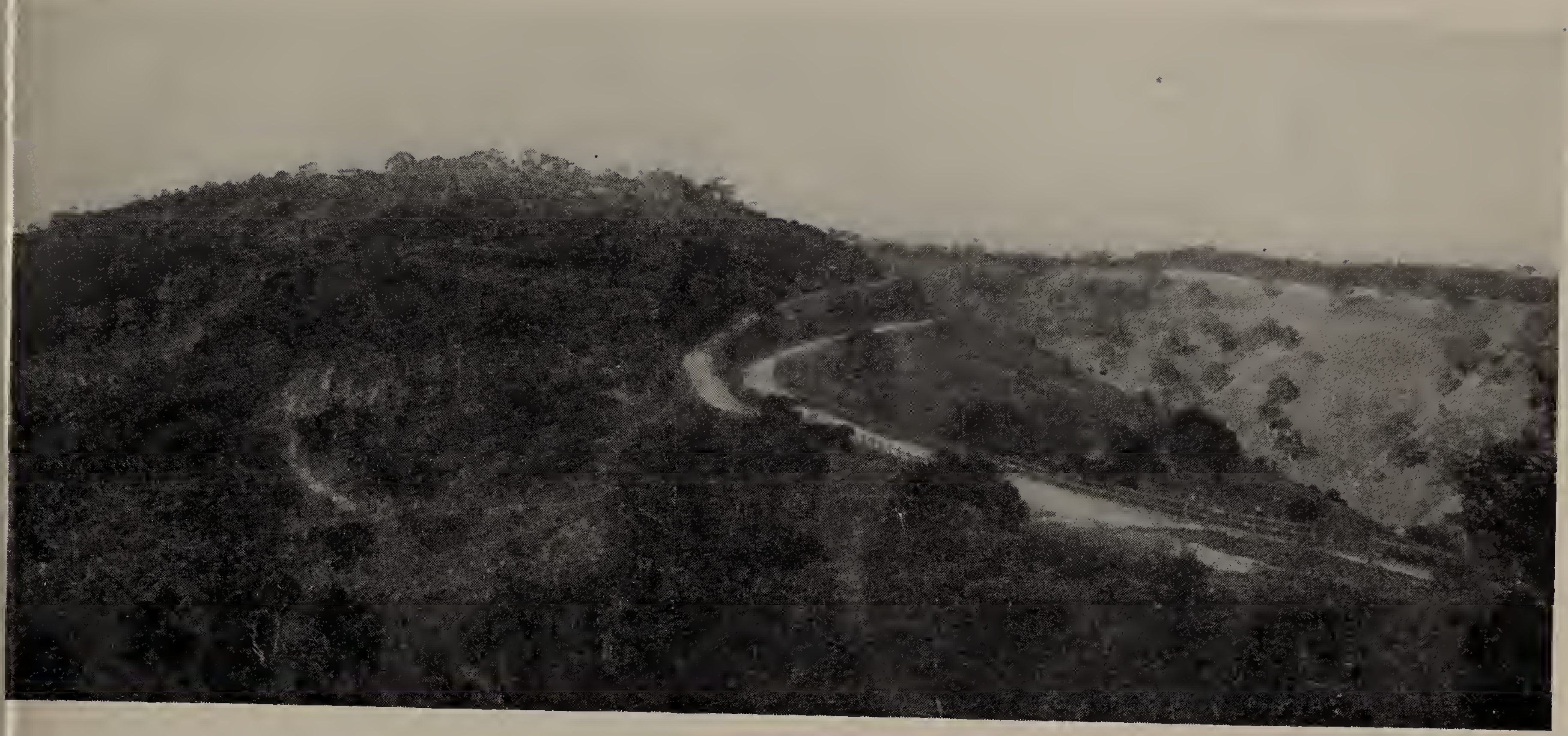


Fig. 1.

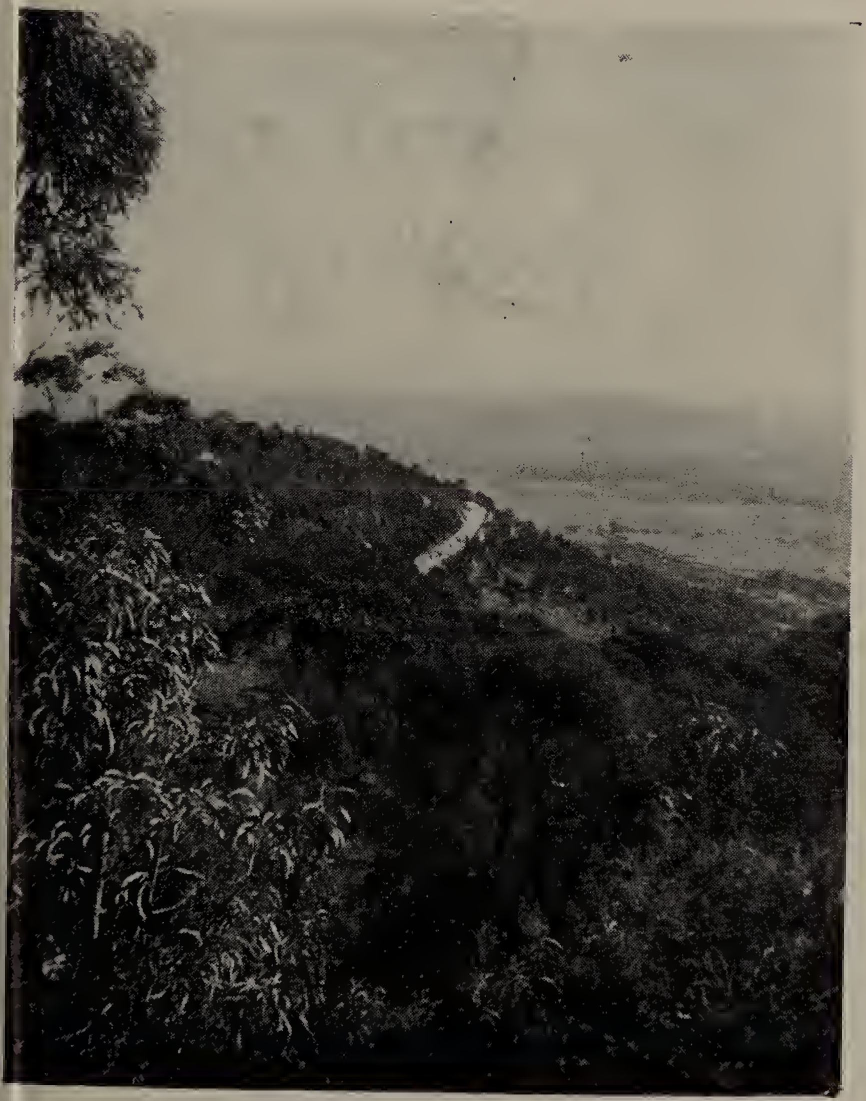


Fig. 2.

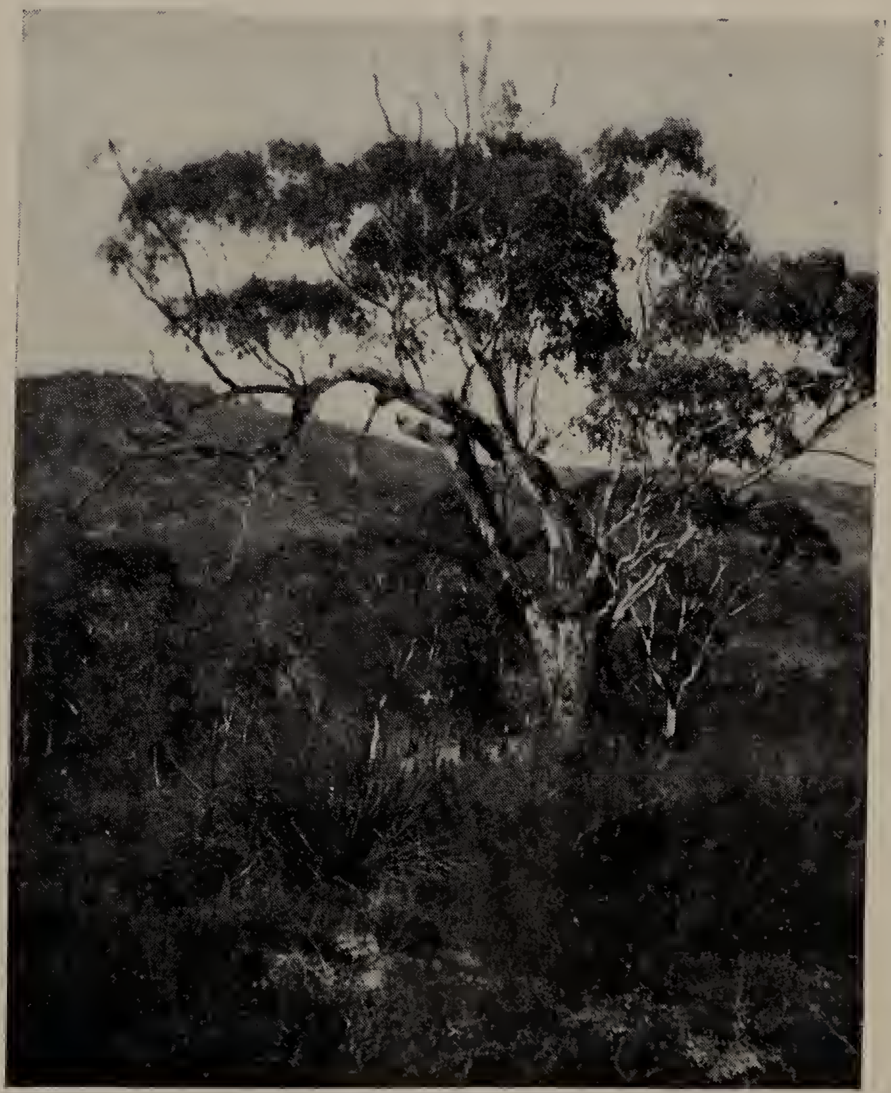


Fig. 3.

OSBORN.—FLORA AROUND ADELAIDE.

THE
NEW PHYTOLOGIST.

VOL. XIII, NOS. 4 & 5. APRIL & MAY, 1914.
[PUBLISHED MAY 25TH, 1914.]

SKETCHES OF VEGETATION AT HOME AND ABROAD.

VIII.—NOTES ON THE FLORA AROUND ADELAIDE, SOUTH AUSTRALIA.

BY T. G. B. OSBORN,

Professor of Botany in the University of Adelaide.

[WITH PLATES I AND II AND THREE FIGURES IN THE TEXT].

INTRODUCTION.

THE following brief account of the vegetation around Adelaide has been written largely as a preliminary to a more detailed ecological study on the district. It is intended merely as a sketch rather than a summary of matured considerations on the subject, since the writer has at present only spent one year in the district. A further inducement to writing has been the fact that Adelaide will be the first point of stay on the forthcoming visit of the British Association in August, 1914.

With the signal exception of Diels' work[1] on the flora of West Australia, the Australian vegetation has been hitherto almost neglected as a field of ecological investigation. The interesting flora of the Mount Kosciusko district of Victoria has been dealt with by Maiden,[2] but that is the only work on ecology of recent years with which I am acquainted. A review of the South Australian flora was made by Schombergk,[3] but his account would be inaccessible to most botanists were it not for a long extract from the more important part in Schimper's Plant Geography,[4] and several references by Diels. Such a lack of information may serve as an additional justification in publishing this sketch.

[1] Diels, L. "Die Pflanzenwelt von West-Australien," 1906.

[2] Maiden, J. H. Agric. Gazette, N.S.W., Vol. 9, 1899, p. 720; Vol. 10, p. 1001, 1900.

[3] Schombergk, R. Flora of South Australia in "South Australia" (edited W. Harcus), 1876.

[4] Schimper, A. F. W. "Plant Geography," 1903, p. 496 and 528 ff.

CLIMATE AND TOPOGRAPHY.

The city of Adelaide, the capital of South Australia, is situated near the eastern shores of St. Vincent's Gulf, lat. 34° 56′ S., long. 138° 35′ E. It stands on an alluvial plain about six miles from the coast at a height of 140 feet above sea level. To the east of the city the Mount Lofty ranges rise by a series of foothills to an altitude of 1900 feet at Mount Lofty eleven miles distant.

The rainfall map of Australia shews that Adelaide stands in the area of winter rainfall, 70% of its total annual precipitation, which averages twenty-one inches, falling between May and October inclusive. Not only are the remainder of the months of the year deficient in rainfall but the temperatures may range very high, 100°F. in the shade being by no means uncommon in December, January or February, while 118°F. has been recorded.[1] The high temperatures are bearable, however, on account of the dryness of the air. The average mean humidity is only 56, while the mean for the two months December and January is as low as 33. Much of the hot season is passed in days of cloudless sunshine. The prevalent wind during the summer months is south-west. This comes moisture-laden from the cool Southern Ocean, but being heated over the land it becomes a drying rather than a rain-bringing wind. Following a well-known cycle the winds periodically shift to the north, becoming intensely hot and dry, and bringing clouds of dust. Under these conditions evaporation rapidly rises but transpiration is not proportionately increased.[2] The total mean yearly evaporation for Adelaide is 54 inches.

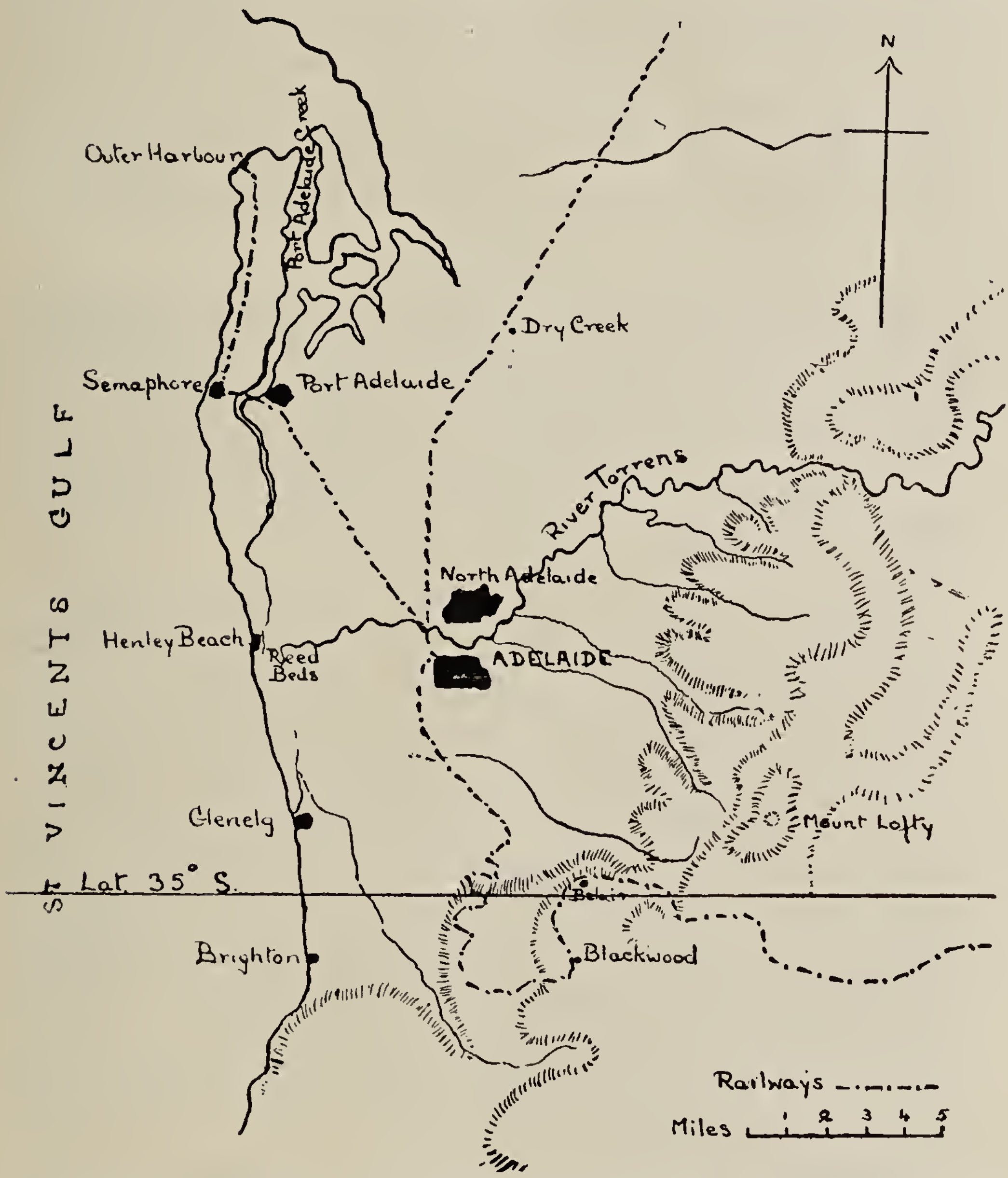
The climatic conditions prevailing in the hills are naturally less extreme, the temperature at Mount Lofty averaging 10°F. cooler than on the plains, while the rainfall is 47 inches. The bulk of the rainfall is in the winter, and the summer months are comparatively hot and dry.

While the climatic conditions favour the production of a flora adapted to xerophytic conditions the geology and topography of the Adelaide district are such that several different formations are to be met with in a comparatively restricted area. The Mount Lofty ranges form the western edge of the South Australian highlands which run in the main north and south. They form one side of the Great Rift Valley of Australia and the same palæozoic strata composing their summits descend in a series of steps to about 2,000 feet below sea level at the coast. The plains on which the city stands begin at the base of low foothills eight miles south of the city and run north for over 100 miles. In origin they are part coastal and part flood. At Adelaide they are crossed by the river Torrens, which rises some 30 miles east and cuts through the ranges in a gorge. In addition there are many "creeks" that rise in the hills which cut deep valleys for themselves before they cross the plain to join the Torrens. For the greater part of the year, though, they are absolutely dry. The Torrens is blocked from the sea by a coast range of sandhills and loses itself in a swampy area, the "Reedbeds," the overflow from which drains into the Port Adelaide

---

[1] These and other meteorological details are taken from "The Climate and Meteorology of Australia," by H. A. Hunt. Bulletin No. 1 of the Commonwealth Bureau of Meteorology, 1911.

[2] Ewart, A. J., and Rees, B. Annals of Botany, Vol. 24, 1910, p. 85.



TEXT-FIG. 1. Sketch map of the Adelaide district. The hills are very roughly indicated, no contoured map being published. Main railways only shown. The suburbs are not indicated.

Creek. This is one of several arms of the sea which lie ten miles north-east of Adelaide and run between mud flats and mangrove swamps. Much of the area that is now land in this region has been submerged in recent times as is indicated by such names as Dry Creek.[1]

The Mount Lofty range consists of a synclinal fold involving rocks of the Cambrian age. The main axis is composed of basal quartzites which have been worn away in places exposing the older grits. The foothills consist for the greater part of the overlying slates. Much faulting has resulted in sharp junctions between slates and quartzite which are noticeable by their different floras.

VEGETATION.

But little remains to show what was the original vegetation of the plains on which Adelaide stands. The evidence is that they were well wooded with various species of *Eucalyptus* (*E. rostrata* by the water courses, *E. viminalis*, and nearing the hills *E. odorata* and *E. leucoxylon*). This is a marked contrast to the Northern portion of the coast plain which was, and still is, almost destitute of trees.

About the coast and around Dry Creek area as well as on certain slopes of the lower foothills were probably many native pines (*Callitris propinqua*), but these are rapidly being exterminated. Amongst the introduced trees the Moreton Bay Fig (*Ficus macrophylla*), pepper trees (*Schinus molle*), *Pinus Halepensis* and *P. insignis* are the most common. Vines, peaches and apricots thrive on the plains, but apples and pears are better grown in the hills. There are extensive orangeries along the Torrens and up the creeks into the foothills, while on the lower slopes are some famous vineyards and olive yards. The paddocks into which the plain is divided are used for wheat (grown in the winter months) and for pasture. The vegetation of the latter is largely composed of alien plants which will be referred to later.

The plains are divided from the sea by a coastal strip. To the north-east lies the Port Adelaide Creek, and numerous other arms of the sea, intersecting low sandy flats. For the greater part of the year they receive little or no fresh water from the rivers draining into them. The muddy banks of the channels are occupied by a thick growth of *Avicennia officinalis* reaching to a height of 12 to 15 feet (Pl. I, Fig. 1). The area immediately behind the mangrove formation is colonised by shrubby Salicornias (*S. arbuscula* and *australis*) associated with *Suæda maritima* and *Samolus repens*. Where the ground is slightly more elevated the Salicornias are replaced by a sward of *Sporobolus virginicus*.

---

[1] Howchin, W. Trans. Roy. Soc. S. Aus., Vol. 30, 1906, p. 227; Vol. 36, 1912, p. 34.

The Dry Creek area which extends three miles inland from the mouth of the Port Creek is interesting, since on it occur Salicornias and other halophytic plants that are relics of the time when the area was subject to tidal inundation.

The coast south of the Port River is bordered by low sandhills. *Spinifex hirsutus*, *Juncus* spp. and *Mesmbryanthemum equilaterale* are the chief sand-building plants, especially the former, on dunes of the more shifting type, but are all markedly inferior to the introduced *Ammophila arenaria* that occurs in places. In addition are numerous shrubs of *Olearia axillaris*, *Styphelia Richeii*, *Scævola crassifolia* and *Pimelia stricta* which in places form a close thicket (Pl. I, Fig. 2). On the more stable sandhills the cyperaceous plant, *Lepidosperma* spp., forms the principal covering over large areas. Behind the sand-hills are swampy areas following the channel of the Torrens to the Port Adelaide creek. These are largely colonised by Salicornias; *Samolus*, *Frankenia*, *Spergularia marina* are also common. The paper bark "ti-trees" (*Melaleuca* spp.) form dense thickets especially by the banks of drainage channels (Pl. I, Fig. 3). They do not, however, replace the mangroves on banks subject to tidal scour.

The lower foothills are occupied by vegetation of two main types. The one is open grassland with Eucalypts (*E. rostrata* and *E. odorata*) and is now largely used for pastoral purposes. This is the commoner type of vegetation and may have been continuous with the woodland of the plains. There are areas, however, where the soil is gravelly (old river gravels) and in such places the grassland disappears to be replaced by scrub of *Eucalyptus* spp., *Acacia* spp., and other shrubs. In such areas many more conspicuous low-growing plants (*e.g.*, the scarlet runner, *Kennedia prostrata*, orchids such as *Caladenia* spp., *Calycothrix*, *Drosera*, *Goodenia*, etc.) are to be found.

The second range of foothills, rising about 800 feet to a plateau, presents several markedly distinct types of vegetation which appear to be correlated with the geological formation. The slate hills are covered with grassland and scattered "gums" having a park-like appearance. The absence of undergrowth and the maintenance of a sward may be partly due to grazing, but all the differences observable cannot be attributed to this cause. Grass is almost entirely absent from the quartzite hills, which are covered by a scrub of many species of shrubby plants. Viewed from the plains the two types of vegetation are clearly distinguishable. The darker olivaceous green of the scrub shows in sharp contrast to the grass covered hills, which are green in the winter but brown in the summer. Where the two strata join a very striking appearance is to be noticed (Pl. II, Fig. 1).

Amongst the more important shrubs of the scrub are species of *Hakea, Banksia* and other Proteaceæ, *Acacia, Pultenea, Dillwynia* and other Leguminosæ, *Styphelia* and *Epacris, Leptospermum* and *Calycothrix*, *Dodonæa*, *Cryptandra* and others in bewildering variety. The general height of such shrubs is about a metre. The ground between them is frequently bare, but many other low shrubby plants (*Grevillea lavandulacea, Pimelia* spp., *Hibbertia* spp., *Goodenia* spp., *Scævola microcarpa*, *Tetratheca*, etc.) occur. In addition are many annuals. These are largely liliaceous or orchidaceous plants in the spring months (August and September) later many Compositæ (*Helichrysum*, etc.) appear.

The "creeks" draining the hills have cut deep "gullies" with precipitous sides in many places (Pl. II, Fig. 2). In the clefts of the rocks *Xanthorrœa quadrangulata* occurs. This is an arborescent form of "grass tree," that may reach two metres to the crown of leaves and not infrequently branches. Its blackened trunks, owing to the burnt leaf-bases, present a grotesque appearance. *Casuarina quadrivalvis* is common along such faces though not confined to them. The lower reaches of the gullies, wherever there is a deposit of alluvial soil, are turned into market gardens, and the native flora destroyed. It must have been in such places that the dense thickets of *Todea africana*[1] occurred, but it is doubtful if any specimens remain wild about Adelaide at the present time.

To the south-east of Adelaide is the Blackwood plateau, the general altitude of which approximates to the higher foothills. Much of this is covered with Eucalypts, with an undergrowth of *Acacia pycnantha*. In certain areas, however, the soil is very sandy (river sands). Here the vegetation becomes more markedly xerophytic and is composed largely of *Lepidosperma* spp., *Casuarina stricta* (a species growing about 1 metre high) and *Hakea ulicina* (Pl. II, Fig. 3).

Ascending the ranges the dominant tree becomes the stringy bark (*Eucalyptus obliqua*) which covers the greater part of Mount

[1] Schombergk, R., *loc. cit.*, p. 213; quoted by Diels, *loc. cit.*, p. 11.

Lofty and its spurs. This tree does not form a close canopy. The undergrowth in the more sheltered places is often *Pteridium aquilinum*. Large areas, however, have a covering of many species of shrubs much as above. In certain areas *Ixodia achilloides*, a composite shrub, some 70-100 cms. high, is the dominant undergrowth. It has sticky decurrent leaves and corymbs of white flowers. A second species of *Xanthorrhœa* (*X. semiplanata*) also occurs in this region, with great frequency in certain places. It does not form an aerial trunk and commonly reproduces by adventitious budding. It is noticeable that this species only flowers at all freely after a fire has swept over the spot. Then it is a remarkable sight to see hundreds of tall erect spikes some 2 to 3 metres high, the upper half covered with white blooms.

It is impossible within the limits of a short sketch to do more than indicate the more important forms of vegetation and a few of the species composing them. There are certain points in connection with the plants mentioned that call for special notice.

LEAF FORM.

The majority of the leaves are hard and tough exhibiting the usual characteristics of evergreen leaves. While some plants, *e.g.*, species of the Proteaceous genera *Hakea*, *Isopogon*, *Banksia*, have markedly xerophytic leaves with thick cuticle, sunken stomata, and reduced leaf surface, others frequently occurring in the same locality have leaves of a less coriacious texture. Such are the leaves of *Bursaria*, *Myoporum*, *Ixodia*, *Dodonœa*. These leaves, however, are frequently sticky and have many sub-epidermal glands.

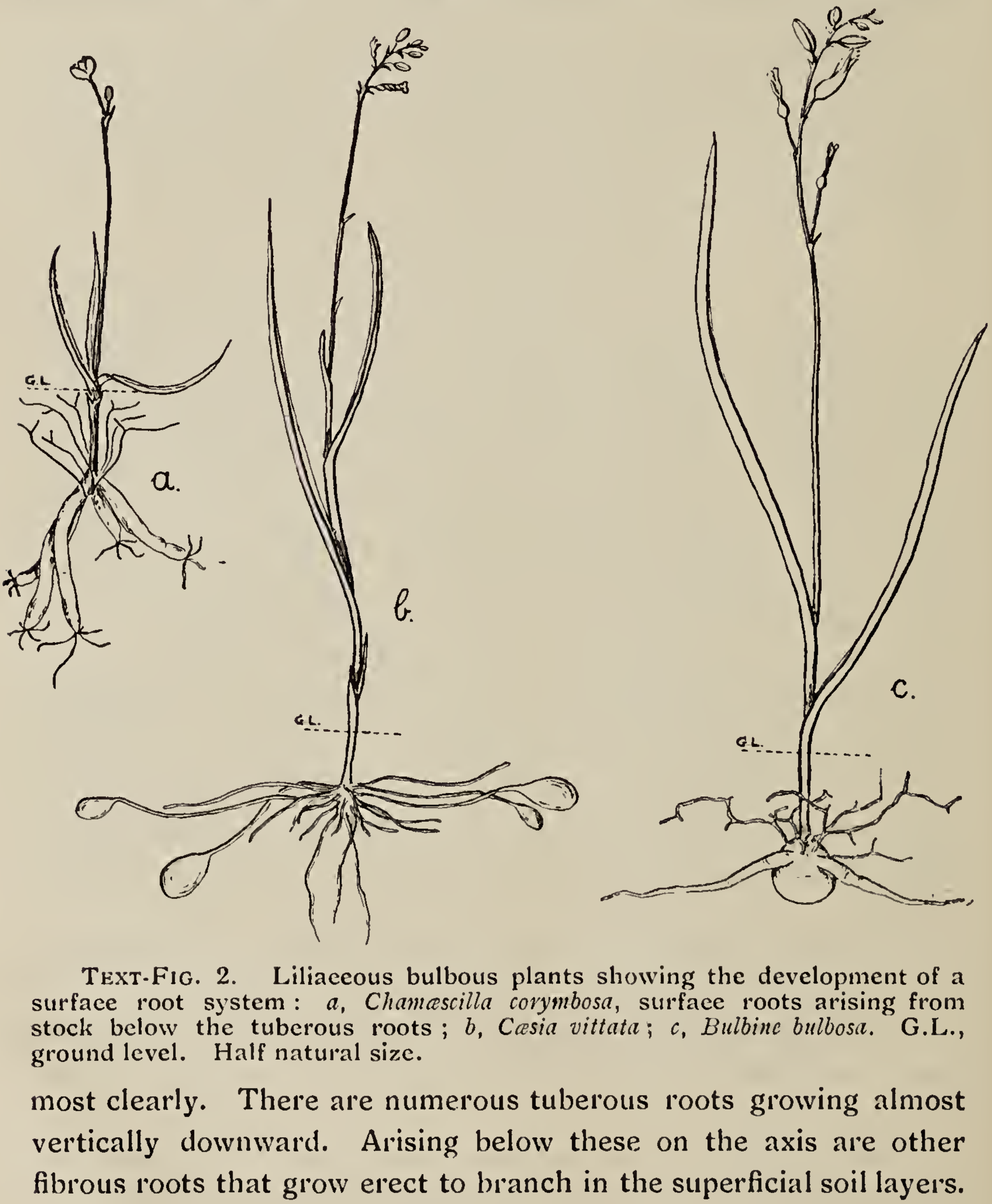
There is a remarkable similarity of leaf-form between plants of widely separated families. The more striking are the pendant sickle-shaped leaves of the Eucalypts and of *Acacia* spp. (e.g., *A. pycnantha*). Leaves of this form are obviously "adapted" to conditions of great insolation. They are also suited to windy conditions, and no one can fail to observe how rare is a perfectly still day.

Obovate to oblong leaves with entire margins are produced by *Dodonœa* spp., *Hakea* spp., *Bursaria*, *Acacia*, *Pultenea*, *Viminaria*, etc., and are strikingly similar in form. Such leaves are frequently placed erect upon the branches so as to expose their edges to the light.

The majority of the leaves on the low-growing shrubs are ovate-lanceolate to linear-lanceolate, rigid, with acute points and about 1 to 2 cm. long. The hairy covering, when present, is often inconspicuous. "Rolled" leaves of the ericoid type are less common than might be expected.

UNDERGROUND STORAGE ORGANS.

A number of the herbaceous plants flowering in September and October have bulbs or other storage organs. Their vegetative season is comparatively brief and they pass the heat of the summer in a dormant state; as examples may be mentioned *Drosera* spp., most Orchidaceæ and Liliaceæ. The development of a surface root system in addition to a deeper one is a notable feature of many Liliaceæ. *Chamæscilla corymbosa* shows this double root system most clearly. There are numerous tuberous roots growing almost vertically downward. Arising below these on the axis are other fibrous roots that grow erect to branch in the superficial soil layers.



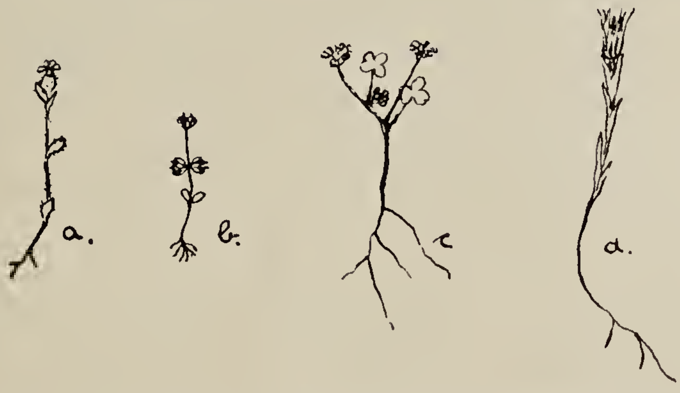
TEXT-FIG. 2. Liliaceous bulbous plants showing the development of a surface root system: *a*, *Chamæscilla corymbosa*, surface roots arising from stock below the tuberous roots; *b*, *Cæsia vittata*; *c*, *Bulbine bulbosa*. G.L., ground level. Half natural size.

Similar phenomena may be seen in *Bulbine bulbosa* and *Cæsia vittata.* Weiss and Yapp[1] have described a rather similar root system in certain plants from the Karroo district, S. Africa.

Several genera of terrestrial orchids form a noticeable feature of the flora in the spring months (September to November). Epiphytic forms on the other hand are entirely absent. The more prominent genera are *Caladenia, Pterostylis* and *Prasophyllum.*

EPHEMERAL PLANTS.

The vegetation of the sandy portions of the plains and foothills is remarkable for the number of extremely minute ephemeral plants that appear in the spring months.[2] The South Australian ephemeral species belong to several natural orders, Portulacaceæ, Saxifragaceæ, Umbelliferæ and Compositæ being largely represented by individuals. It is noticeable that while some of the species, e.g., *Leewenhœkia dubia, Hydrocotyle callicarpa,* appear only to occur in this minute form, this is not the case with all. In many cases plants of reduced size, showing cotyledons still green on a plant in flower or even fruit, may be found almost side by side with others of the same species that have attained the full vegetative development of the species (e.g., *Claytonia volubilis, Podotheca angustifolia, Mellotia tenuifolia*). While the greater number of the species of ephemerals appear to be native to South Australia, others, as *Cryptostemma, Hypochœris* and *Briza maxima* among the introduced plants occasionally adapt themselves to a very brief vegetative period.



TEXT-FIG. 3. Ephemeral plants from lower foothills: *a, Leewenhœkia dubia* (Stylidiaceæ); *b, Tillæa purpurata* (Crassulaceæ); *c, Hydrocotyle-callicarpa* (Umbelliferæ); *d, Quinetia Urvillei* (Compositæ). All natural size.

---

[1] Weiss, F. E., and Yapp, R.H., NEW PHYTOLOGIST, vol. 5, 1906, p. 101.

[2] Cf. Weiss, F. E., and Yapp, R. H., *loc. cit.*, p. 105.

PTERIDOPHYTA.

Vascular cryptogams are poorly represented around Adelaide. *Pteridium* has already been mentioned. *Cheilanthes tenuifolia* is a common fern on the foothills, where it may cover large areas. *Adiantum æthiopicum* is still to be found though in decreasing amounts. *Grammitis rutæfolia* and *Asplenium flabellifolium* are not uncommon in the crevices of rocks by the creeks. Schombergk refers to thickets of *Todea* of which probably no specimen survives wild to-day. *Gleichenia circinata* is now only rarely to be found in the damper places.

PARASITIC PLANTS.

Certain phanerogamic parasites are noticeable features of the vegetation. *Exocarpus cupressiformis* occurs frequently in the hills. Even more notable are species of *Loranthus* and *Cassytha*. *Loranthus pendulus* is common on Eucalypts, huge masses of its yellowish green foliage hanging in profusion from many trees. The leaves of this species are very similar to those of the host plant in shape and pendent habit. *Cassytha pubescens* occurs in great profusion on a large number of hosts. Though frequently referred to as "Australian dodder" it has but the most superficial resemblance to *Cuscuta* since, though leafless, it is green. Like *Loranthus* the fruits of *Cassytha* have a glutinous pericarp that readily adheres to anything in which it may be placed. Once established the plant spreads rapidly by means of its tough twine-like stems. A second species, *C. glabella*, is more common on the lower growing shrubs, e.g., *Pultenea*, *Epacris*, *Hibbertia*, etc. Autoparasitism is extremely common amongst *Cassytha* stems which frequently form rope-like masses as much as a centimeter thick.

FIRES.

Bush fires are only too common even in the settled districts of the hills. It is well known that the hard woody fruits of *Hakea* and *Banksia* may normally remain closed for many years but open freely after a fire. The stringybark, *Eucalyptus obliqua*, shoots freely from dormant buds even after a severe scorching. It is probable that seedling Eucalypts only have a good chance of establishing themselves when a fire has cleared the ground. I have repeatedly observed, especially on a visit to the extreme south-east of the State, that all the trees or saplings over a large area appear to be the same age, while standing amongst them will be the burnt trunks of older trees. The flowering of *Xanthorrhœa semiplanata* after a fire has already been noticed. Two orchids, *Lyperanthes nigricans* and *Prasophyllum elatum*, are practically never found in flower except on burnt scrub.[1]

PERIOD OF FLOWERING, ETC.

The spring months, August, September and October, are the chief months in which the native plants flower. Early in November, as the hot weather approaches, there is a marked diminution in the number of species in flower. Many Compositæ and Goodeniaceæ persist through the summer. *Lobelia gibbosa* and *Dipodium punctatum* both flower in the extreme heat of December and January. The former has a long fleshy flower stalk bearing the racemose inflorescence, buds on which will open and flower standing in a dry test-tube in the laboratory a month after the specimen has been collected. *Dipodium* is an orchid bearing a long leafless scape, nor are there any visible leaves. It has been suggested that this is parasitic on the roots of Eucalypts, but no satisfactory evidence has been obtained.[2]

The colour, scent and honey produced by most flowers indicate insect pollination. Except for the Gramineæ, *Callitris* and *Casuarina* are the only common anemophilous plants. The possibility of bird pollination is a matter that needs investigation. I have repeatedly observed honeysuckers perched upon the inflorescences of *Xanthorrhœa*, *Callistemon* and *Banksia*.

The pollen of the Acacias and the Proteaceæ (notably *Hakea* and *Banksia*) is freely exposed though the flowers are not wind pollinated. Willis[3] notes this as a peculiarity to be connected with their life in a dry climate, but it is notable that most of the Acacias about Adelaide flower in August and September during the close of the wet season when their flowers must often be drenched with rain. The same applies to *Hakea rostrata*, *H. ulicina* and *H. rugosa*. These latter plants, however, like *Banksia*, upon which Bentham[4] has commented, form remarkably few fruits, a fact possibly not wholly correlated with their pollen mechanism since *Grevillea lavendulacea* seeds freely. Lepidopterous insects are uncommon, there is only one species of butterfly at all frequent about Adelaide, but night-flying moths are numerous. Far more common are various Hymenoptera and Diptera which frequently visit flowers.

---

[1] I am indebted to Dr. Rogers of Adelaide for this information.

[2] Rogers, R. S. "Introduction to the study of South Australian Orchids." Adelaide Education Department, 1911.

[3] Willis, J. C. "Manual and Dictionary of Flowering Plants and Ferns," 1904, p. 530.

[4] Bentham, G. Journ. Linn. Soc., vol. 13, p. 58.

ALIEN PLANTS.

It is only to be expected that in the neighbourhood of a large city and the chief port of a State, alien plants should be numerous. This is the case in the vicinity of Adelaide where over 300 species are recorded as established. The country of origin of most of these plants is interesting. Black[1] gives the following records :—Europe generally, 128 ; Mediterranean region, 92 ; Cosmopolitan, 60 ; South Africa, 44 ; Temperate South America, 15. He remarks, " It is noticeable that the plants which succeed best in the struggle for life are those which come from lands with climates resembling our own." The ability of alien species to compete successfully with native plants is the subject of some discussion. It is popularly believed that in many cases the alien is able to establish itself so successfully as to oust the native plant. Cockayne,[2] writing of the phenomena to be observed in New Zealand, states that only where man has produced entirely new conditions can the alien succeed in doing so. In other places "invader and aboriginal have met and, though the original vegetation is changed, there is no reason to consider the one class or the other as the conqueror."

It is certainly true that as weeds of cultivation and of pasture many aliens have most successfully established themselves in the Adelaide district. Among the former *Oxalis cernua*, *Antirrhinum orontium* and *Inula graveolens* must be mentioned. *Inula* is specially noticeable in February and March, when whole paddocks may be covered by it so as to exclude other vegetation. The greater part of the pasture vegetation is composed of alien plants, and, as little or no attempt has been made to introduce grasses, weeds are very common. The "Cape Dandelion" (*Cryptostemma calendulacea*) covers acres that in September are a sheet of gold with its blooms. *Erodium moschatum*, *E. Botrys* and *Stachys arvensis* form the chief plants over large areas. Many Mediterranean and South African bulbous or corm-producing plants are to be found, in places in such numbers as to be a pest. Such are *Asphodelus fistulosus* and *Romulea cruciata*, while species of *Moræa*, *Sparaxis*, *Iris*, *Homeria* and *Muscari* also occur. On certain parts of the hills *Rosa rubiginosa* is common, scattered over the paddocks or forming thickets. *Aloë*, *Agave* and *Opuntia* have all been used as hedge plants at different times but their rate of spread is not rapid.

---

[1] Black, J. M. "Naturalised Flora of South Australia." Adelaide, 1909, p. 3.

[2] Cockayne, L. " The Flora of New Zealand." The New Zealand Handbook, 1912.

The above plants, however, have all taken possession of land on which man, by cultivation, has produced a set of conditions that are foreign to the native species. There are, however, examples of alien plants that maintain themselves side by side with the original flora when the latter has not been subjected to a severe change of conditions. *Gomphocarpus* occurs commonly in the scrub on the foothills. The creeks have proved channels of invasion of much of the hills area. *Nasturtium officinale* and *Mentha viridis*, especially the latter, may be found in the beds of streams far above the area under constant occupation. In many districts of the hills *Cytisus canariensis* quickly invades any burnt scrub or may even capture areas where no fire has prepared a way.

I am indebted to my wife for the drawings forming text-figures 2 and 3, and for assistance in many other ways.

THE BOTANICAL LABORATORY,
ADELAIDE UNIVERSITY,
October, 1913.

EXPLANATION OF PLATES I AND II.

PLATE I.

FIG. 1. Mangrove swamp near mouth of Port Adelaide Creek. The mangroves (*Avicennia officinalis*) are following a small drainage channel. The ground vegetation in the left of the foreground is *Salicornia australis*. On the left can also be seen part of a bush of *Salicornia arbuscula* nearly a metre high.

FIG. 2. Sand-hill vegetation near Brighton. The photograph shows a valley between two ranges of dunes. In the foreground *Spinifex hirsutus*. The bushes are largely *Olearia axillaris* and *Scævola crassifolia*.

FIG. 3. View from sandhills looking inland across drainage channel from Reed beds to Port Adelaide creek. The trees are *Melaleuca* spp. growing along channel and round brackish pools. The undergrowth is *Salicornia* spp., *Samolus*, etc.

PLATE II.

FIG. 1. Junction of quartzite (left) and slate and limestone (right). The precipitous face to the left with *Casuarina* and *Dodonæa* shows in sharp contrast to the grassy slopes on the right.

FIG. 2. View from a head of a gully looking over the plain. Vegetation in foreground *Acacia pycnantha* (left) and *Casuarina*. In the distance the level plain, under cultivation, can be distinguished.

FIG. 3. Scrub on river sands of Blackwood plateau. *Lepidosperma* and small shrubs in foreground, centre (left) *Xanthorrhœa semiplanata* (right) *Hakea ulicina*.

FURTHER OBSERVATIONS ON *HIRNEOLA AURICULA-JUDÆ* BERK. ("JEW'S EAR").

By M. J. Le Goc, B.A.,

Botany School, University of Cambridge.

[With Nine Figures in the Text].

SINCE my preliminary observations on *Hirneola auricula-judæ* were published (1) further observations have brought to light some new features in the biology of this fungus, while the details then described have been more carefully investigated by myself. Also Mr. Brooks has called my attention tof three additional papers on this fungus (10, 15, 16) which are specially interesting because they provide us with two different versions of many important phases in the life-history of the Jew's Ear fungus. It is, therefore, with the hope of bringing forward some fuller information and of elucidating some controverted points that these further observations, are now published. Fries refers to the Jew's Ear fungus as "antiquitus celebrato"; this celebrity of the fungus was due to its supposed medicinal properties, for on account of its fanciful resemblance to the fauces, it was frequently used as a cure for sore-throat in the days when the external form of a plant was thought to be a sufficient guarantee for its therapeutic quality. According to Berkeley, it was occasionally sold at Covent Garden for such a purpose as late as 1857.

The Jew's Ear fungus received several different names: *Tremella auricula judæ* (12), *Exidia auricula judæ* (6, p. 221; 1, p. 355), *Exidia auriformis*, *Auricularia sambucina* (13, p. 459), etc., until Fries and Berkeley fixed the name *Hirneola auricula-judæ* (7, 8, 2). The last name though more generally accepted has found a rival in *Auricularia auricula-judæ* used more especially by German writers (10, 15, 16). *Hirneola* is derived from "hirnula," a small jug; *auricula* (from *auris*, an ear (has been attached to it throughout its history on account of the ear-like form it often assumes (cf. Fig.1); while *judæ* is said to refer to the host, the Elder tree, on which the legend represents Judas as having hanged himself. The popular name of "Jew's ear" is a corruption of Judas' ear.

Brefeld (3), Moller (15, 16) and Holtermann (10) in their study of the biology of this fungus have confined their work to the germination of the spores and the structure of the fructifications.

As is well known the Jew's ear fungus belongs to the Auriculariaceæ, a group of the Basidiomycetes characterized by transversely septate basidia arranged in a definite hymenium which becomes freely exposed during spore formation (9, 18). The structure of the hymenium, of the basidia, and the formation of basidiospores has been carefully described by Brefeld (3) and as my investigations agree exactly with his, I need not repeat what is well known.

This fungus is of wide distribution, both in the tropical and temperate regions. It is of frequent occurence in the neighbourhood of Cambridge. At a young stage it is little differentiated, and consists of cylindrical or roundish masses, several of these often gathered closely together and not infrequently connected at the base (Fig. 2). There is a tendency for the young fructifications to assume a more or less vertical position; but later on they extend horizontally thus allowing the spores to fall more easily, in order to be carried away and be dispersed by the wind. The upper surface is hairy and brown with a tinge of green, but I have never observed olive green specimens as described by Brefeld (3). The lower surface containing the hymenium is of a deeper brown, sometimes blackish, often folded in the manner of a human ear. Some

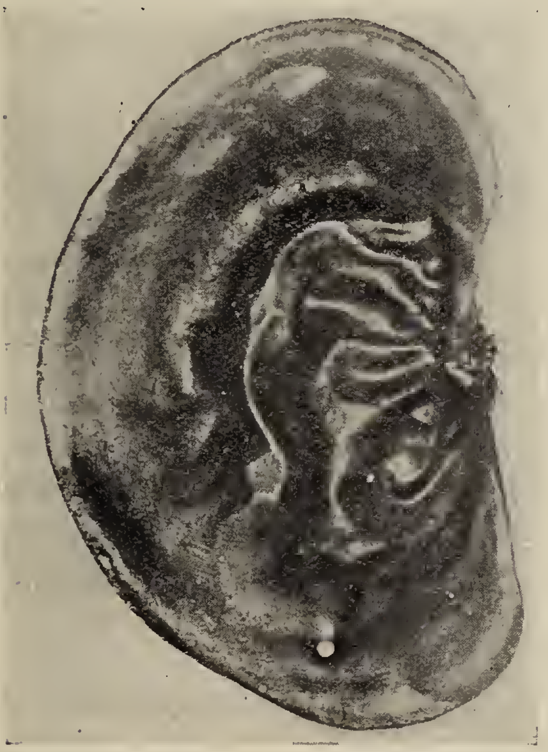


FIG. 1.

FIG. 1. Fructification of *Hirneola auricula-judæ* imitatinga human ear. Nat. size.

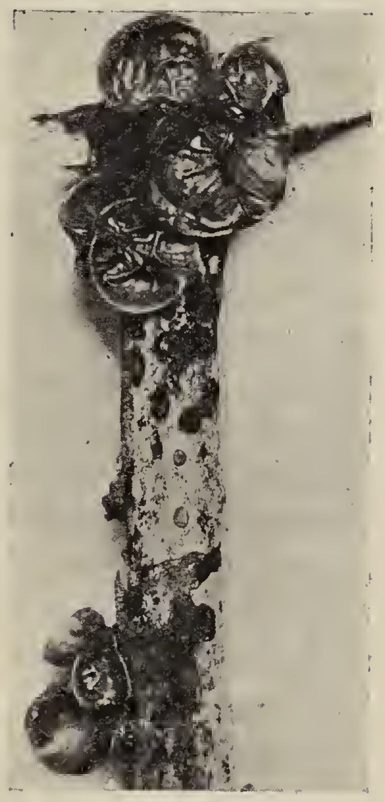


FIG. 2.

FIG. 2. Groups of fructifications on a dead twig of Elder. Nat. size.

forms have been found by Möller showing polyporoid tendencies. Möller says (15, p. 164) " Das Hymenium kann ganz glatt, thelephoreenartig sein, dann durch Falten gerunzelt, endlich sogar regelmassig netzig grubig polyporeen-artig."

Most of the material used has been collected from the vicinity of Byron's Pool near Cambridge. It is found abundantly on Elder bushes, both living and dead, and also on dead branches and trunks of Elm trees in moist places. It has been suggested that the *Hirneola* growing on Elm is perhaps not identical with the *Hirneola* which grows on Elder. In the specimens I examined the hymenium is decidedly freer from folds, but as a matter of fact spores from *Hirneola* on Elder have germinated quite easily and grown quite happily on blocks of Elm wood. It is also usually stated that the fructifications reach a size varying from 4 cm. to 7 cm. in diameter. (14, p. 404), but it is often much larger and a specimen collected in this locality measured 21·6 cm. by 12 cm.

The fructifications which are gelatinous under moist conditions shrivel to black horny masses in a dry atmosphere. In this form the fructifications remain alive at least twelve months, because after this interval they revive again when moistened and produce an abundant supply of spores—a phenomenon also exemplified by *Stereum purpureum* and some other fungi (4, p. 143; 5, p. 106). A fructification which has been soaked in water for some 10 minutes produces spores after an interval of some 10 hours, which can be made to fall on sterilized glass slides, where they form a thick white deposit. They can thus be transferred into tubes of sterilized water or directly picked up with a sterilized platinum needle and used for cultures.

GERMINATION OF SPORES ON THE FRUCTIFICATIONS.

If the fruit body is kept moist for two or three days and the spores allowed to accumulate on its surface, it is found that they germinate *in situ*. The mycelia reach a considerable length, and in course of time form protuberances projecting from the surface of the fructification. These projections prove to be webs of hyphæ entangled together, and enclosing a large number of ungerminated spores, some of them in a good state of preservation. The hyphæ themselves soon undergo a process of disintegration indicated by the glycogen breaking into small globules regularly arranged in a chaplet which simulates a chain of " oidia." Some of the ungerminated spores look healthy after a lapse of three months and are capable of germination if introduced into a suitable nutritive solution. Spores kept on a dry plate loss their vitality more quickly, being more exposed to desiccation, and refuse to germinate a month after liberation.

GERMINATION OF SPORES IN LIQUIDS.

There is a great difference between the results obtained by Brefeld and Möller on the one hand and by Holtermann on the other.

Möller (16) attributes the difference to lack of accuracy in Holtermann's work. I must confess that without any previous knowledge of Holtermann's paper, I published observations which were exactly similar and often expressed in phrases which look like a free translation from Holtermann. Such an agreement is of considerable interest and shews that Möller's explanation of the divergent results is not tenable. It is worth while quoting Holtermann himself (10, pp. 41-42) who describes in concise and clear language the points of difference between the two sets of observations. "Brefeld asserts that the spores germinate easily in water as well as in nutritive solutions by emitting germination threads which branch irregularly and frequently near their point of origin. At

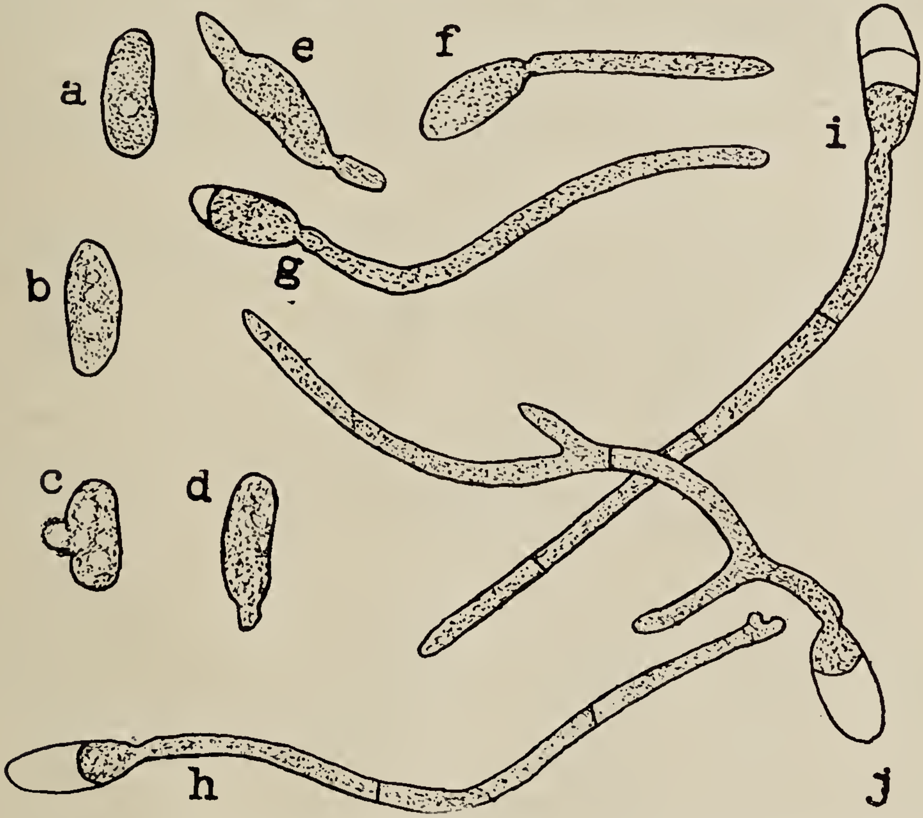


FIG. 3. Basidiospores of *Hirneola* in decoction of Elder wood : *a*, healthy spore ; *b—c*, spores undergoing disintegration ; *d*, *f—j*, germinating spores ; *e*, germ tubes at both ends. × 600.

the extremities of the ateral outgrowths minute conidia are formed. Besides I refer to his own work on this question (Brefeld, VII, p. 73). Only I note that by supplying a richer nutritive solution, according to Brefeld, other branchings and branching systems are laid down as conidiophores. Möller insists on Brefeld's statement and has also obtained a more or less abundant production of the characteristically hooked conidia. Unfortunately he gives no drawings to confirm this point. As already mentioned I obtained different results. I have not even succeeded in bringing out the germination of spores in water. As Brefeld states that often eight days or more are required before germination begins to become later on general, I left the spores often three weeks; but of conidia formation there was no trace to be observed. On the contrary, the spores became divided by partition walls and emitted germination tubes; but in spite of every attempt, any further formation failed."

Like Holtermann I repeatedly tried to get results agreeing with those of Brefeld, but always failed in my attempts, at least as far as nutritive solutions were concerned.

The spores were cultivated in hanging drops in sealed cells, and easily observed under the microscope.

Experiments were carried out in strong, medium and weak light, and even in darkness. Under these conditions germination was never observed in hanging drops of water, but in Elder wood decoctions it occurred occasionally.

However, if a drop of the decoction is laid at the bottom of the same cell instead of being suspended from the cover glass, germination takes place regularly. The probable explanation of this anomally is that the spores being heavier than the liquid fall to the bottom, so that in the hanging-drop cultures the spores are only partly immersed and osmosis is not carried out in the normal manner. In tubes or watch glasses the spores germinate very readily in Elderwood decoction, and rarely in distilled water. Like Holtermann I found that the spores germinate on the third day, but if the spores had not germinated by this time further development was impossible even after allowing them an opportunity which lasted more than a fortnight. Invariably after some five days drops of glycogen were formed in any ungerminated spores which at a later stage became ruptured and emitted their contents (Fig. 3, b,c). Brefeld, on the contrary, observed spores often germinating after being immersed for a period lasting more than eight days (3, p. 72).

Brefeld also describes as of regular occurence the formation of conidia on the germinating spores in water or in nutritive solutions (3, pp. 73-76). In my own observations conidia were sometimes obtained in water either directly from the spores (Fig. 4, b,c) or from the hyphae which were first produced (Fig. 4, d,e), they occured one day or two after the spores had commenced to germinate, *i.e.*, on the fourth or fifth day of immersion. But they have never been seen in nutritive solutions either concentrated or dilute, and whenever conidia were suspected they proved to be, on close examination, hooks or clamps by means of which the hyphæ are kept entangled together. I may add that the hooked conidia produced in water are somewhat different from those sketched by Brefeld (3, pl. IV) their curvature being less marked (Fig. 4, f.)

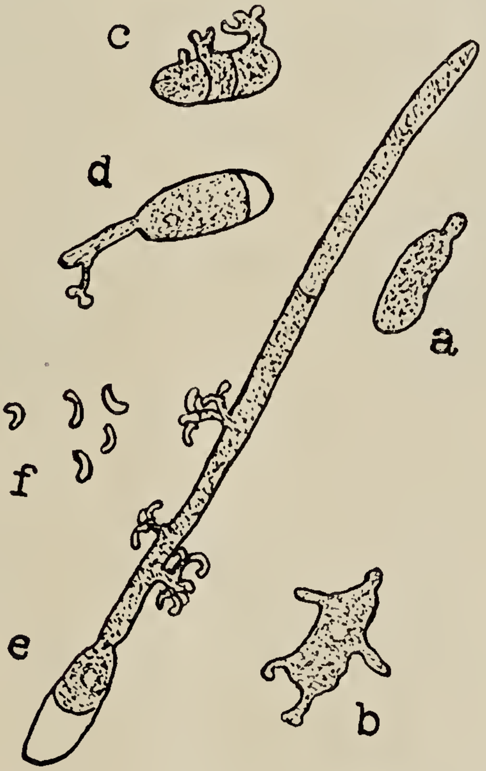


Fig. 4. Basidiospores germinating in distilled water and giving rise to conidia seen in different stages of development : *b—c*, conidia produced directly from the spores ; *d—e*, conidia borne on hyphæ ; *f*, mature conidia. × 600.

Thus Möller's prophecy that "the inexactitude of Holtermann's statements would be shown in course of time through the further researches of other workers" (16) has not been entirely fulfilled as far as my observations are concerned, though I have been dealing with a European form of the Jew's Ear fungus.

It is far from me, however, to say that Möller's results are inexact. It is better to take facts as they have been observed than to state that results different from our own are impossible or inaccurate. This divergence of results is perhaps an instructive disagreement. It allows us to suggest that we may be dealing here with two different strains of the same fungus.

This difference of behaviour of the same species of fungus is not unique and it is a phenomenon which deserves to be still more generally investigated. Shear and Wood (17, p. 98) have given an interesting example in the fungus *Glomerella cingulata* and conclude that " the production or non-production of the perithecial stage of *Glomerella* seems to be a fairly well fixed hereditary race character." The results of investigations on the fungus *Hirneola auricula-judae* point to the existence of two strains of this species which behave somewhat differently from one another.

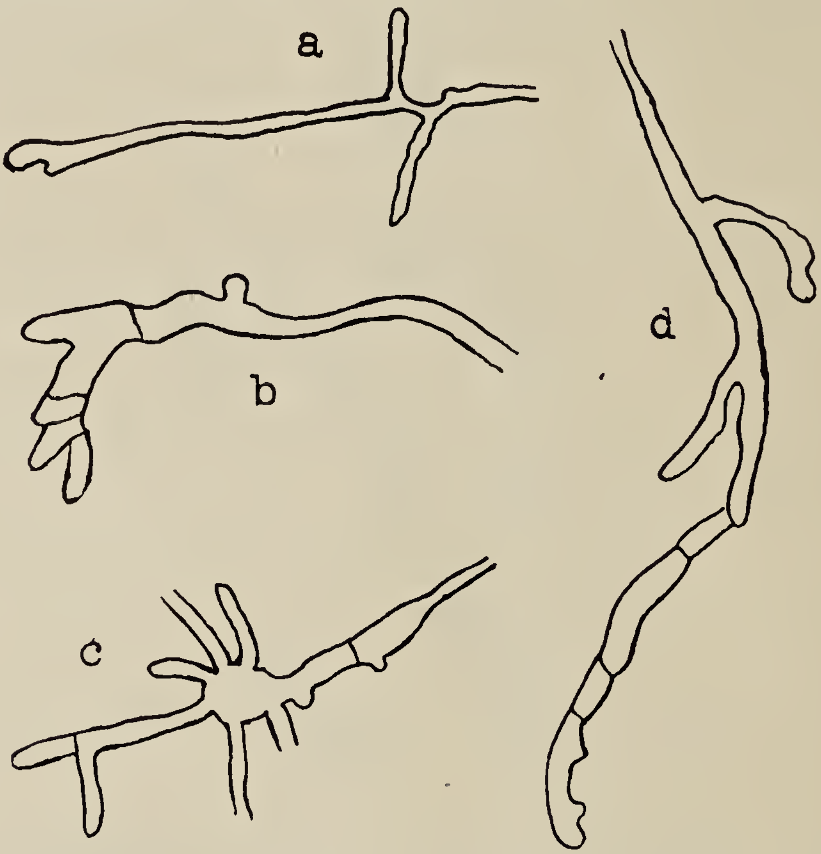


FIG. 5. Stout irregular hyphæ in Elder wood decoction+gelatine. ×600.

PURE CULTURES OF THE FUNGUS.

(a) *Cultures in decoctions of Elderwood+agar or gelatine.* Elderwood decoction was solidified with 2% agar or 10% gelatine after previous sterilization by the usual methods. Plate cultures were obtained in the usual manner. In agar cultures the spores germinate quite easily and after some fifteen days patches of mycelia become visible to the naked eye. These mycelia grow with some difficulty and not always with equal success. Cultures ten months old show no attempt to produce fructifications.

The cultures on gelatine are more interesting and show an almost luxuriant growth. At first a woolly layer of mycelium appears on the surface but the gelatine is soon liquified, and the fungus sinks into the medium, assuming a definite form and developing into bodies which imitate in shape the fructifications of the Jew's Ear fungus. Those bodies form gelatinous, compact masses, built of fine thin threads mixed with not a few stout irregular hyphae, which branch freely in all directions (Fig. 5). No definite hymenium has been observed and these structures are not likely to develop further. Still the production of a rudimentary fruit-body within a liquid is interesting and unusual in the higher fungi.

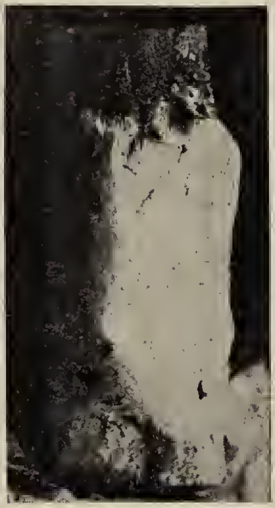


FIG. 6. Woolly texture of fungus enveloping a block of Elder wood in artificial culture. Nat. size.

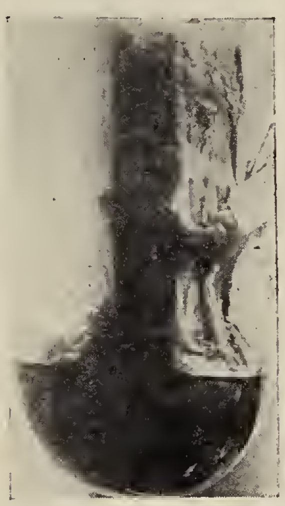


FIG. 7. Rudimentary fruit body produced on block of Elder wood in artificial culture. Nat. size.

(b) *Cultures on wood.* Pure cultures of the fungus have been established on blocks of Elder, Lime and Elm wood about 5 cm. in length and from 1 to 4 cm. in diameter. These blocks of wood were enclosed in tubes or flasks containing a certain amount of water and sterilized in the usual manner. Inoculation of the blocks of wood has been effected by transferring to them spores deposited on sterilized glass slides or mycelia derived from pure cultures. With few exceptions the inoculations have been successful After three weeks a white woolly outgrowth appears on the spots infected and spreads quickly all round the blocks, forming a thick envelope (Fig. 6). This white woolly envelope shows at times signs of active growth indicated by large drops either of a clear or brownish liquid which is oozed out as in the well-known example of *Pilobolus*.

At this stage large, stout, irregular hyphæ are found in abundance, and of the type described in the cultures on gelatine (Fig. 5). This active growth preceeds the formation of fruit bodies.

Fructifications have commenced to develop on several blocks (Fig. 7) exposed to light of moderate intensity, but they have not proceeded very far; no definite hymenium on basidia have been observed, and these rudimentary fructifications consist only of compact gelatinous masses of interwoven hyphæ. The mycelia covering the blocks kept in a dark room have made no attempt to produce such fruit bodies, but have grown luxuriantly and spread as a white snow-like layer over the whole of the bottom of the flasks.

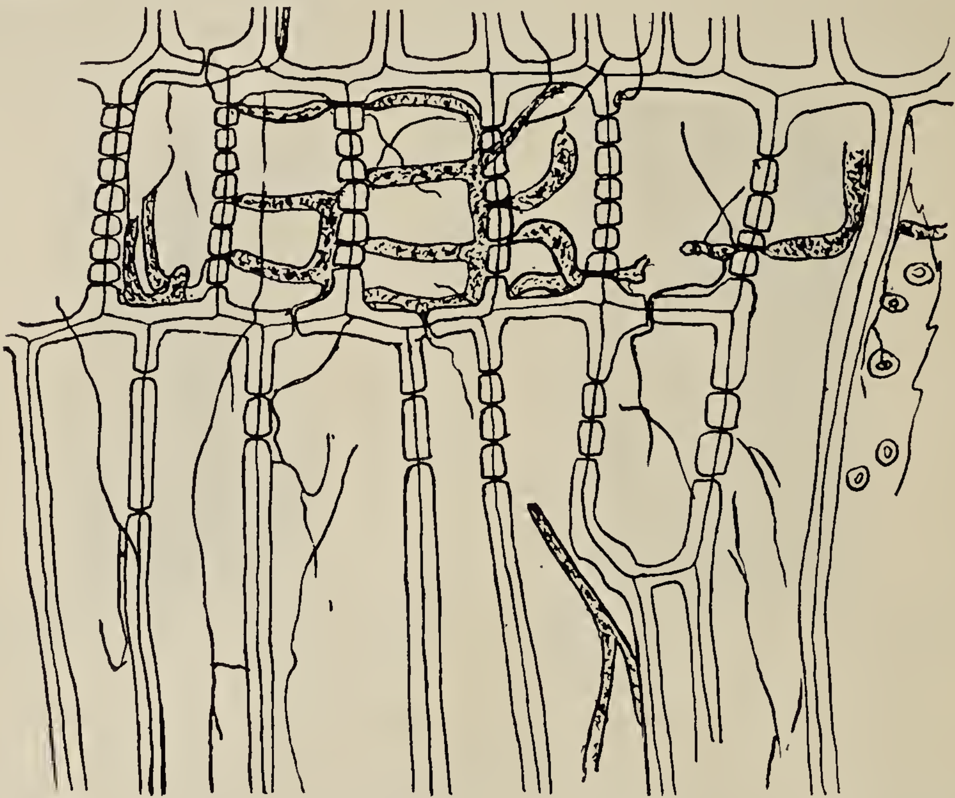


FIG. 8. Longitudinal section of inoculated Elder twig. Stout and thin hyphæ passing through the pits. Stout hyphæ present in greater numbers in short cells. ×600.

The penetration of hyphæ inside the wood used in these cultures has been tested at intervals. It is very rapid and after three months the hyphæ have run all through the tissues. The path followed is along the vessels and tracheids with penetration through the pits, and more frequent branchings in the medullary rays or in the short cells (Fig. 8). In long tracheids we often observe only one thread of mycelium, at least in an early stage. For some time the fungus seems to be satisfied with the food found inside the cells, but when hunger presses hard on the fungus it encroaches on the cell walls, beginning by the pits, which become enlarged until the wall between them is consumed (Fig. 9). The xylem is delignified, the hyphæ bore their way locally through the walls which are gradually eaten up. Staining at this stage shows patches of wood entirely delignified among patches still exhibiting the presence of lignin, the whole appearance being that of a very inartistic mosaic. Schulze's solution is very convenient for revealing the action of the fungus, but Cotton Red and Aniline Blue are more effective, because they stain the hyphae blue and allow one to observe more closely the delignification in relation to the presence of the fungus. From an investigation of twigs affected by the fungus in nature the ultimate result is seen to be that the whole tissue becomes spongy, crumbles when rubbed with the finger, and consists as much of the hyphæ as of the original tissue of the tree.

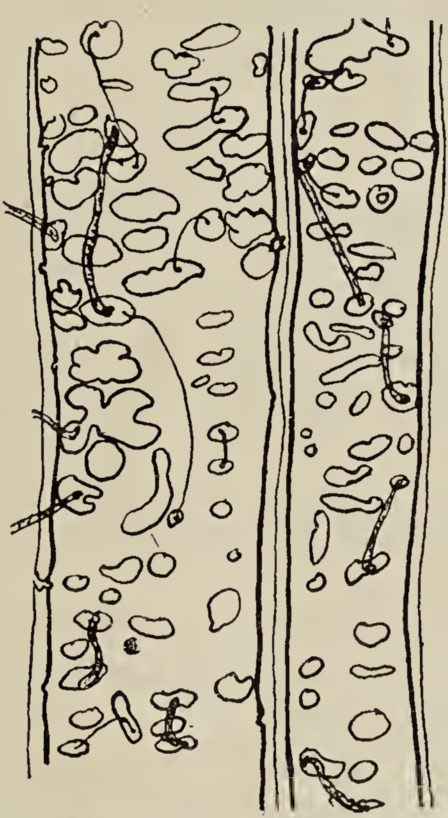


FIG. 9. Longitudinal section of Elder twig infested by the fungus, from nature. Walls of vessels delignified and in places entirely eaten up by mycelium. × 600.

INOCULATIONS OF ELDER BUSHES WITH THE FUNGUS.

This part of the experiments have been carried out at St. Edmund's House, Cambridge, by kind permission of the Master, the Rev. T. L. Williams. Inoculations with mycelia and spores have been made in living branches of Elder bushes by making T-shaped cuts in twigs of the thickness of a finger and enclosing in them by means of a platinum needle, a few threads of mycelia, or in other instances a drop of sterilized distilled water containing spores in suspension. The wounds were then protected with tin foil.

Many of these inoculations have proved successful. The spores germinated and the mycelia penetrated the wood in the manner just described (Fig 8), the only difference being that the process of penetration is at first very slow. But after some months the tissues near the place of inoculation are killed and appear blackish-grey; the function of the conducting tissue is interfered with, and consequently growth is impeded and the ultimate result is the death of the twig, giving the fungus an opportunity of working freely at the destruction of the wood and of penetrating quickly the vessels and other elements through the pits. The section drawn in Fig. 8 is taken at 5 cm. from the place of inoculation after an interval of ten months; closer to the wound the work of the fungus is more advanced, resulting in the disorganisation of the tissues.

SUMMARY.

1. Germination of spores of the Jew's Ear fungus takes place readily and occurs even *in situ* on the fructifications, if these are kept moist for several days.
2. Germination and growth of basidiospores are of general occurrence in suitable nutritive solutions, but occur less frequently in distilled water.
3. Conidia are produced rarely in the material used in this investigation and only in distilled water; these conidia germinate rapidly.
4. Cultures in decoctions of Elder wood + agar or gelatine develop well. Gelatine is liquified and rudimentary fruit bodies are produced inside the liquid.
5. The fungus grows readily on Elder, Lime and Elm wood in pure culture, resulting in the production of rudimentary fructifications if exposed to a fair amount of light.
6. The penetration of hyphæ inside the tissues is very rapid resulting in the delignification of the wood which in the case of naturally-infected wood is ultimately almost entirely consumed.
7. Inoculations on healthy living twigs of Elder were successful in many instances; penetration by the hyphæ was at first very slow, but later on the twigs were killed.

I wish to express my hearty thanks to Mr. F. T. Brooks for suggesting this work and for his kind guidance during the progress of the investigations.

LITERATURE CITED.

1. Berkeley, M. J. "Cryptogamic Botany," 1857.
2. ——— "Outlines of British Fungology," 1860.
3. Brefeld, O. "Untersuchungen aus dem Gesammtgebiete der Mykologie." Heft VII, pp. 70-76.
4. Brooks, F. T. "Silver-leaf Disease." Journ. Agric. Sci., vol. IV, 1911.
5. Buller, A. H. R. "Researches on Fungi," 1909.
6. Fries, E. "System a mycologicum." II.
7. ——— "Hymenomycetes europæi," 1874.
8. ——— "Fung. Nat."
9. Fuckel, L. "Symbolæ mycol.," 1869.
10. Holtermann, C. "Mykologische Untersuchungen aus den Tropen." Berlin, 1898, pp. 37-43.
11. Le Goc, M. J. "Observations on *Hirneola auricula-judæ*." Proc. Camb. Phil. Soc., vol. XVII, Part 3, 1913, pp. 225-8.
12. Linnæus, C. "Species Plantarum," 1625.
13. Martius, K. F. "Fl. crypt. Erl.," 1817.
14. Massee, G. "Diseases of Cultivated Plants and Trees," 1910.
15. Möller, A. "Protobasidiomyceten." Jena, 1895, pp. 42, 164.
16. ——— "Phycomyceten und Ascomyceten. Untersuchungen aus Brasiliens." Jena, 1901, pp. 37-43.
17. Shear, L. A., and Anna K. Wood. "Studies of Fungous Parasites belonging to the genus *Glomerella*." U.S. Dept. of Agric., Bur. of Plant Industry, 1912.
18. Winter, G. "Die Pilze Deutschlands, Oesterreichs und der Schweiz," 1884.

THE WHITE MOSS LOCH:
A STUDY IN BIOTIC SUCCESSION.

By J. R. Matthews, M.A.,

Assistant Lecturer in Botany, Birkbeck College, London.

[With Two Figures in the Text].

Introductory.

THE White Moss Loch or the White Moss, as it is locally called, is a small sheet of water situated about two miles west of Dunning in Strathearn, Perthshire, Mid-Scotland. In 1901, according to the ordnance Survey of that year, the water covered an area of a little over 16 acres (*c.* 6·5 hectares). The land immediately surrounding the open water, being unsuitable for cultivation, has been fenced off, and in area measured (in 1901) about 7 acres (*c.* 2·8 h.). A map of the area under consideration is shown in Fig. 1, the boundary line indicating the fence. About thirty years ago the land within the fence was partly planted up with trees and the writer is informed that the inmost line of trees, consisting chiefly of willows, was placed as near the water's edge as possible. This inner tree limit is shown on the map by a black wavy line. The above information and the nature of subsequent events compel one to conclude that, when the trees were planted, a comparatively narrow space was left between the tree line and the water margin. But by a gradual process of centripetal encroachment of various plants there has arisen a fairly wide zone of marsh and swamp vegetation between the tree line and the present position of the open water. The process is still going on; the width of the marshy shores continues to increase, while there is a corresponding diminution of the area under water, which at present does not exceed 10 acres (*c.* 4 h.).

Although the marsh and swamp vegetation is of limited extent, it shows in its development a definite succession of plant communities, and the consequent change in the general aspect of the loch is exceedingly striking. The succession has been under observation for several years, and the present account is an attempt to give some idea of the process and of the part played by the different plant communities that occur.

Geology, Climate and Rainfall of the District.

The loch lies in a natural depression 0·75 mile (*c.* 1,200 m.) to the north of the Ochil Hills. This depression occurs at the end of a branch from a secondary valley which runs along the foot of the hills. At its nearest point the river Earn, which finds its course through the main valley of the Strath, is 1·25 mile (*c.* 2,000 m.) north of the loch. From present conditions it is difficult to say whether a stream of any size ever followed the valley in which the loch is situated. If so, the direction would be from west to north-east, but at present the valley to the north-east becomes constricted and only a ditch leading from the loch occupies its bottom. As has happened in other parts of the country it is probable that cultivation of the surrounding land has considerably altered the physiographic features.

Although so near the Ochils, the loch is not associated with the andesitic lavas of these hills, but rests on the Old Red Sandstone at an elevation of 175 feet (*c.* 53 m.) above sea level. Mud consisting of fine particles of sand mixed with much organic material covers the bottom to a depth of at least two metres. There is no inflow stream, but a ditch at the west end conducts into the loch a considerable amount of surface drainage during the winter months. The surrounding fields slope towards the loch which thus receives most of their drainage. There are several springs in the vicinity and these may help to maintain a supply of water. The outlet at the north-east corner is also artificial and only during winter does water escape in any quantity. From the rapid deposition of organic material at the bottom it is evident that at one time the loch was deeper than it is now. At present the water is nowhere more than a metre deep during the summer months, although in winter the depth may be almost twice this. The bottom is the shape of a shallow saucer, and if all the water could be drained off, a comparatively flat expanse of loose organic mud would remain.

The following data regarding rainfall and temperatures for the district have been obtained from observations taken over the past twelve years.

The average annual rainfall is 38·5 inches (*c.* 980 mm.). The winter months are the wettest, and thus the water level is highest when the temperature is lowest. The average of the mean daily temperatures is 46°F. (7·7°C.). In 1911, 87·2°F. (30·6°C.) was recorded as the maximum for the year and for the period during which observations have been made. The average of yearly absolute maximum temperatures is only 73°F. (22·7°C.). The absolute

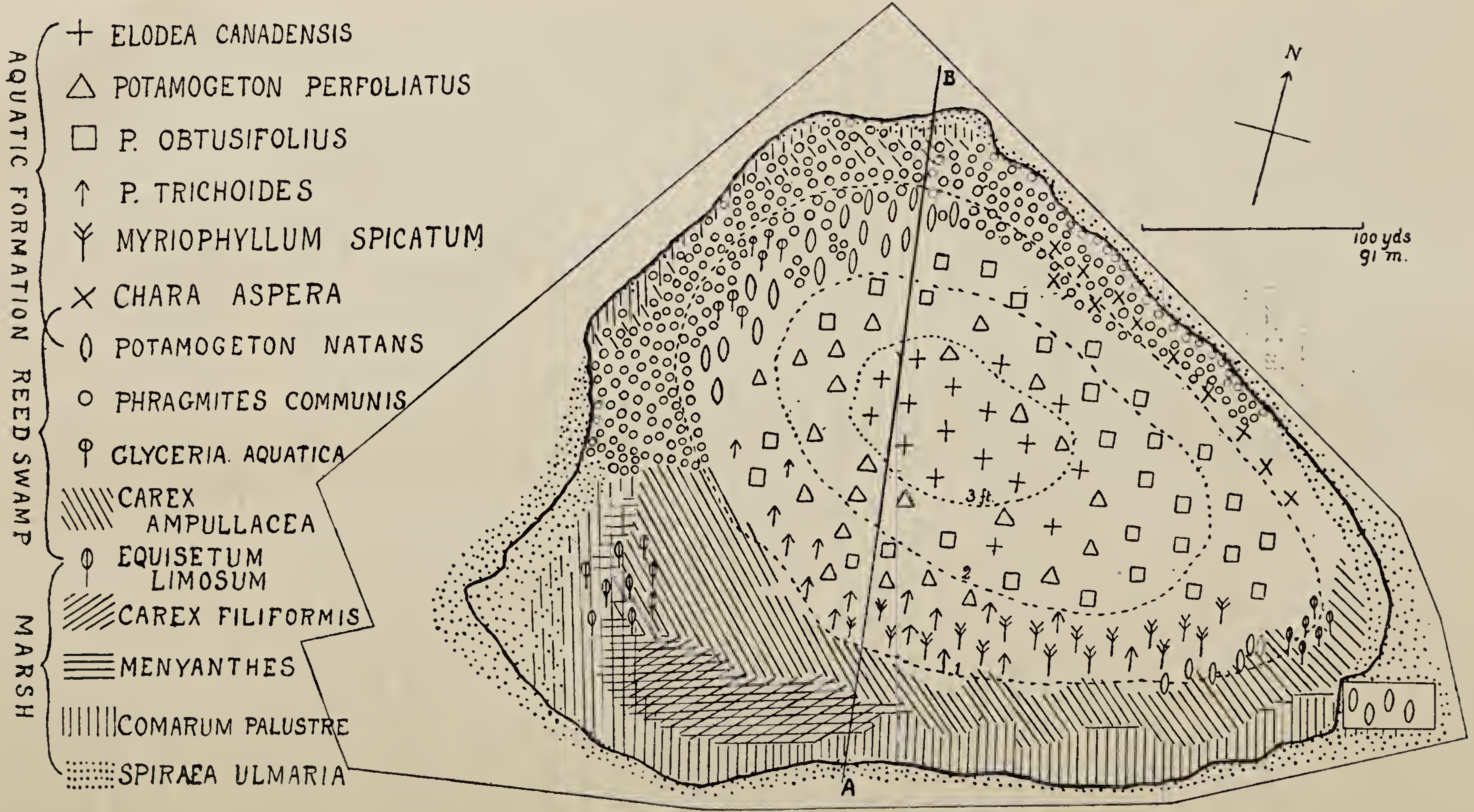


FIG. 1. Map of the White Moss to show distribution of the plant communities and their dominant species (from observations made in August, 1913).

minimum annual temperatures average 9·7°F. (—12·5°C.), but in January, 1910,—4°F. (—20°C.) was recorded. In this year (1910) the loch was ice-bound for six weeks, but usually the period during which the water is frozen does not exceed two weeks.

THE PLANT COMMUNITIES.

It is evident that the vegetation of the open water does not belong to the same formation as the vegetation of the surrounding marsh. The first and last stages in the succession from open water to marsh cannot be included in the same formation, but since these stages are gradual it is difficult to decide which of the various stages shall be included in the one formation and which shall be included in the other.[1] This difficulty applies to the reed-swamp community more than to any other, but for reasons given by Miss Pallis[2] the generally accepted classification is followed and reed-swamp is regarded as the terminal association of the aquatic formation. The vegetation of the White Moss may therefore be arranged under two headings:—

I. AQUATIC FORMATION. II. MARSH FORMATION.

The distribution of the plant communities and the dominant species forming these communities are indicated on the accompanying map (Fig. 1). Because of its importance as a transitional stage and for the sake of clearness the reed-swamp with its constituent species has been shown separately from the aquatic formation. As already pointed out, however, its status is that of association. A complete bathymetrical survey of the loch was not made, so the contour lines on the map to show depth of water are only approximate.

I.—AQUATIC FORMATION.

Although the water is nowhere deep, the distribution of the true aquatics suggests their classification into associations according to depth of water. Three associations may therefore be distinguished. (A) **Deep water association,** (B) **Shallow water association,** (C) **Reed-swamp association.**

(A). **Deep water association.** The deepest part occurs about the centre of the loch, but slightly nearer the north side than the south. The depth is here about 1 m. and *Elodea canadensis* Michx. is dominant. The plants are remarkably tall and erect and have very long internodes. Very few species are associated with *Elodea*, and free floating plants in any part of the loch are absent. *Utricularia vulgaris* L. has been recorded,[1] but all endeavours on the part of the writer to find this plant ended in failure.[2]

---

[1] C. E. Moss. "The Fundamental Units of Vegetation." NEW PHYTOLOGIST, Vol. 9, 1910, p. 37.

[2] M. Pallis, in "Types of British Vegetation," 1911, p. 223.

The following plants occur in this association :—

Elodea canadensis **d.**
Potamogeton filiformis **f.**
Nitella translucens **f.**
Potamogeton perfoliatus **o.**

(B). **Shallow water association.** In the shallower water bordering on the reed-swamp and to some extent amongst the plants of this zone there is a greater abundance of aquatics. Towards the north side *Potamogeton natans* L. is dominant, with a few species of *Nitella* growing on the mud bottom. Towards the south side of the open water *Myriophyllum spicatum* L. is dominant, and with this plant there is a greater number of associated species occupying the floor of the loch. This lower storey consists chiefly of *Potamogeton trichoides* Cham.,[3] *P. perfoliatus* L. and *Nitella opaca* Ag. Along the east side and extending among the plants of the reed-swamp the bottom is carpeted with *Chara aspera* var. *subinermis* Kuetz. These three locally dominant species may be regarded as forming three societies in the shallow water association.

The complete list is as follows :—

Potamogeton natans **l.d.**
Myriophyllum spicatum **l.d.**
Chara aspera var. subinermis **l.d.**
Potamogeton perfoliatus **a.**
P. trichoides **a.**
P. obtusifolius **a.**
Myriophyllum alternifolium **f.**
Nitella opaca **f.**
N. flexilis var. crassa **f.**
Potamogeton heterophyllus **f.**

(C). **Reed-swamp association.** As already indicated the reed-swamp occupies the shallower water round the shores forming a zonal community characteristic of lowland lochs.[4] The zone is sharply divided into two regions—one to the north side of the loch, dominated by *Phragmites communis* Trin., the other to the south side, dominated by *Carex ampullacea* Good. (see map, Fig. 1). Moreover, *Phragmites* is entirely absent on the south side, but on the north side the sedge is associated with the reed to a small extent. The habitat is the same in both cases and it is difficult to say what factor has determined the distribution. The distribution is therefore interesting, for it shows the same habitat dominated in one place by a single species and in another place by a different species. Divisions of an association dominated by different species have been described by Gleason[1] and Gates[2] under the term *consocies.* Gleason, in the part of his paper which deals with prairie formation, recognises four *consocies* in the bunch-grass association. In the area investigated by Gates two *consocies* of the bunch-grass association are described. While the secondary species remain the same, the dominant species in each of these smaller units (*consocies*) of the association are different, although there is no obvious difference in their environments. This is a new use of the term *consocies.* It was originally used by Clements[3] as synonymous with association, but in its new sense it is particularly useful and descriptive. The term may be applied to describe the two areas into which the reed-swamp association is divided, and since *Phragmites* and *Carex* are the alternative dominants, the divisions may be designated (*a*) *Phragmites communis* consocies, (*b*) *Carex ampullacea* consocies.

---

[1] F. B. White. "Flora of Perthshire," 1898.

[2] J. R. Matthews. "Notes on Mid-Perth Plants." Journ. Bot., Vol. 51, 1913, p. 193.

[3] The first record for Scotland. See note by A. Bennett in Journal of Botany, Vol. 41, 1913, p. 336. And for a full account of the distribution of this species see A. Bennett, "*Potamogeton trichoides* in Perthshire," Trans. Perth. Soc. Nat. Sci., 1913-14 (in the press).

[4] R. and W. G. Smith. "Botanical Survey of Scotland: Forfar and Fife." Scot. Geog. Mag., 1905, p. 74.

(*a*) *Phragmites communis consocies.* Throughout this zone the common reed is dominant in some places quite to the tree line. At two places on the inner margin of the swamp small societies of *Glyceria aquatica* Wahlb. occur. Eastwards the zone becomes narrower and the *Chara* already mentioned in describing the shallow water association forms a dense growth on the sandy bottom. Nearer the shore where the water is still shallower the ground vegetation consists of *Litorella lacustris* L.

At a few places just within the tree line plants of lower growth than the reed are becoming more abundant, indicating the beginnings of a marsh community. The chief invading plant is *Comarum palustre* L. and probably time will bring about the dominance of such humbler plants while the reeds will continue to advance inwards. This is already shown by the occurrence of two reed islands which have established themselves in the open water (Map, Fig. 1). There is a distinct tendency, however, for the reed to persist long after the surface of the soil is raised above the water level, perhaps because its subterranean organs are still placed in a saturated soil[1] (see section, Fig. 2). Thus, when once established the reed holds its own for a long time and this seems to explain why marsh vegetation is less developed on the north than on the south and west sides of the loch. The floristic composition of the *Phragmites consocies* is as follows:—

---

[1] H. A. Gleason. "The Vegetation of the Inland Sand Deposits of Illinois." Bull. Illinois State Lab. Nat. Hist., Vol. 9, 1910, p. 23.

[2] F. C. Gates. "The Vegetation of the Beach Area in N.E. Illinois and S.E. Wisconsin." *Ibid.*, Vol. 9, 1912, p. 255.

[3] F. E. Clements. "Research Methods in Ecology." Lincoln, Neb., U.S.A, 1905. Mr. Tansley informs me that Professor Clements now proposes to use the term in the newer sense indicated above.

Phragmites communis **d.**
Glyceria aquatica **l.d.**
Carex ampullacea **a.**
Litorella lacustris **a.**
Equisetum limosum **l.a.**
Carex flava **o.**
Alisma ranunculoides **o.**

(b) *Carex ampullacea consocies.* This forms the terminal zone of the aquatic formation on the south and west sides of the loch. It is a marked feature of the vegetation extending 350 yards(320 m.) in length, and consists entirely of tussocks of *Carex ampullacea* except at points near the two extremities. At these points *Equisetum limosum* becomes sub-dominant, and in addition there is near the eastern extremity a small patch of *Sparganium ramosum.* The plants extend into fairly deep water and at one place *Potamogeton natans* finds shelter. Landwards this community passes into the marsh formation and on this side of the loch the dividing line between swamp and marsh is remarkably distinct. No other species except those already mentioned occur in the *Carex ampullacea* consocies.

II.—MARSH FORMATION.

The marsh formation includes those plant communities which succeed the reed-swamp and terminate in the narrow belt of willow and alder which forms the inner tree limit. It has already been pointed out that the marsh forms only a narrow zone round the landward side of the reed-swamp to the north and east of the loch, but on the south and west sides marsh vegetation is of greater extent. The nature of the vegetation is determined by the saturated condition of the soil, but the water level is probably responsible for marked differences in the floristic composition of the smaller divisions of the formation. Two associations may be recognised—(A) **Herbaceous marsh association,** (B) **Alder willow association.** The former succeeds the reed-swamp; the latter is the present terminal association of the marsh.

(A). **Herbaceous marsh association.** In the successional development of this community a definite process takes place, in which two plants, *Menyanthes trifoliata* L. and *Comarum palustre*

---

[1] R. H. Yapp. "Sketches of Vegetation at Home and Abroad: Wicken Fen." NEW PHYTOLOGIST, Vol. 7, 1908, p. 76.

L. play an important rôle. Further, the species associated with these two plants are different, so that two divisions of the herbaceous marsh association appear. These may be designated (a) *Carex-Menyanthes sub-association*, (b) *Comarum palustre sub-association*.

(a) *Carex-Menyanthes sub-association.* This community is chiefly developed on the south side and immediately succeeds the *Carex ampullacea consocies.* By the gradual deposition of plant remains in the *Carex ampullacea* community the level of the organic material forming the substratum is raised and when the depth of water does not exceed a few centimetres (five to six) *Menyanthes trifoliata* appears. When this stage is reached, *Carex ampullacea* is no longer dominant but is co-dominant with the *Menyanthes.* The community formed is quite distinct but is now limited to a narrow zone between the *Carex ampullacea consocies* and the *Comarum sub-association.* Some years ago it was much more extensive. At one place on the south side, however, is has remained unaltered for a considerable time, but here it is *Carex filiformis* which is associated with *Menyanthes* (see Map, Fig. 1). Whatever be the biological differences between this sedge and *C. ampullacea* it certainly forms a community with the bogbean which resists very successfully the invasion of other plants. The following species occur in this sub-association :—

Carex ampullacea **d.**
Menyanthes trifoliata **d.**
Carex filiformis **l.d.**
Equisetum limosum **l.a.**
Comarum palustre **f.**
Epilobium palustre **o.**

(b) *Comarum palustre sub-association.* After a few years the accumulation of decayed vegetable matter amongst the intertwining rhizomes of *Menyanthes* forms a drier carpet of vegetation, and the *Carex-Menyanthes* community becomes invaded by *Comarum palustre.* In its initial stages this process is aided by a species of *Vaucheria.* For a year or two *Comarum, Menyanthes* and *Carex* exist together, but ultimately the first gains dominance and the *Menyanthes* entirely disappears. Thus the next community in the successional order—the *Comarum palustre sub-association*—is formed. Repeated observations of the process have been made, and it can be distinctly traced at one or two places on the west side of the loch. The subterranean parts of *Comarum* become covered by a rapid growth of mosses, particularly *Mnium punctatum, Hypnum cordifolium* and *H. cuspidatum.*[1] The mosses undoubtedly do much to prepare the ground for other plants, for almost invariably it was among them that seedlings were observed. It seems that the majority of these seedlings, however, do not attain full development, for it is a striking feature that wherever *Comarum palustre* is dominant very few other species are associated with it. This is a marked feature along the south side. At places on the west side *Juncus acutiflorus* Ehrb. and *Mentha aquatica* var. *major* Sole. become locally dominant and with these the number of social species is greater. The list for the sub-association is as follows:—

---

[1] As determined by Mr. Meldrum.

Comarum palustre **d.**
Mentha aquatica var. major **l.d.**
Juncus acutiflorus **l.d.**
Galium palustre **a.**
Agrostis alba **a.**
Equisetum limosum **a.**
Spiræa Ulmaria **f.**
Myosotis cæspitosa **f.**
Potamogeton polygonifolius **f.**
Carex ampullacea **f.**
Ranunculus flammula **o.**
Epilobium palustre **o.**
Juncus conglomeratus **o.**
Juncus effusus **o.**
Carex teretiuscula **o.**
C. panicea **o.**
C. flava **o.**
Pedicularis palustris **r.**
Veronica scutellata **r.**

(B). **Alder-Willow Association.** The trees of this association, forming a fringe round the loch, have been planted, but since the habitat is quite a natural one for the species that occur, and since self-sown bushes of willow have appeared, it seems desirable to separate this community as an association distinct from the herbaceous marsh. The surface of the soil is higher above the ground water-level than in the herbaceous marsh, and this probably accounts for a difference in the floristic composition of the ground vegetation. The most remarkable feature is the suppression of *Comarum palustre* and the dominance of *Spiræa Ulmaria.*

The following trees occur:—

Salix caprea **a.**
S. viminalis **a.**
S. cinerea **f.**
Alnus rotundifolia **f.**
Populus sp. **f.**
Salix purpurea **r.**

The ground vegetation consists of the following species:—

Spiræa Ulmaria **d.**
Aira cæspitosa **s.d.**
Galium palustre **a.**
Hydrocotyle vulgaris **a.**
Mentha sativa **a.**
Myosotis cæspitosa **a.**
Iris pseud-acorus **l.a.**
Nasturtium officinale **f.**
Juncus acutiflorus **f.**
Holcus lanatus **f.**
Equisetum sylvaticum **f.**
Caltha palustris **o.**
Cardamine pratensis **o.**
Viola palustris **o.**
Epilobium tetragonum **o.**
Angelica sylvestris **o.**

Vicia cracca **f.**
Lotus uliginosus **f.**
Geum rivale **f.**
Scabiosa succisa **f.**
Mentha aquatica var. major **f.**
Achillea Ptarmica **o.**
Briza media **o.**
Dactylis glomerata **o.**
Orchis mascula **r.**
Listera ovata **r.**

The following are frequent species which have probably come in from the surrounding arable land :—

Senecio Jacobæa **f.**
Centaurea nigra **f,**
Plantago lanceolata **f.**
Rhinanthus Crista-galli **f.**
Cnicus arvensis **f.**
Bartsia Odontites **f.**
Euphrasia officinalis **f.**

The following is a summary of the plant communities distinguished in the vegetation of the White Moss :—

I.—AQUATIC FORMATION.

(A). **Deep water association.**
(B). **Shallow water association.**
(C). **Reed-swamp association.**
  (a) Phragmites communis consocies.
  (b) Carex ampullacea consocies.

II.—MARSH FORMATION.

(A). **Herbaceous marsh association.**
  (a) Carex-Menyanthes sub-association.
  (b) Comarum palustre sub-association.
(B). **Alder-Willow association.**

DISTRIBUTION OF THE PLANT COMMUNITIES AND THE DETERMINING FACTORS.

In considering the factors which have determined the plant distribution, the chemical constitution of the soil and water may be regarded as remaining fairly uniform throughout, since there is no inflow stream, there is no differentiation of soil salts or of æration between different parts of the loch. Lime is present in the water to a small extent and the decaying vegetation in itself returns nutriment to the soil. There seems to be sufficient evidence for regarding the main determining factors as entirely biotic.[1]

In the aquatic formation, only submerged plants occur in the deepest water, but the accumulation of their débris results in a shallowing of the water and in the shallower zones floating plants develop. The open water on the north side is sheltered from the

---

[1] H. C. Cowles. "The Causes of Vegetative Cycles." Bot. Gaz., Vol. 51, 1911, p. 171.

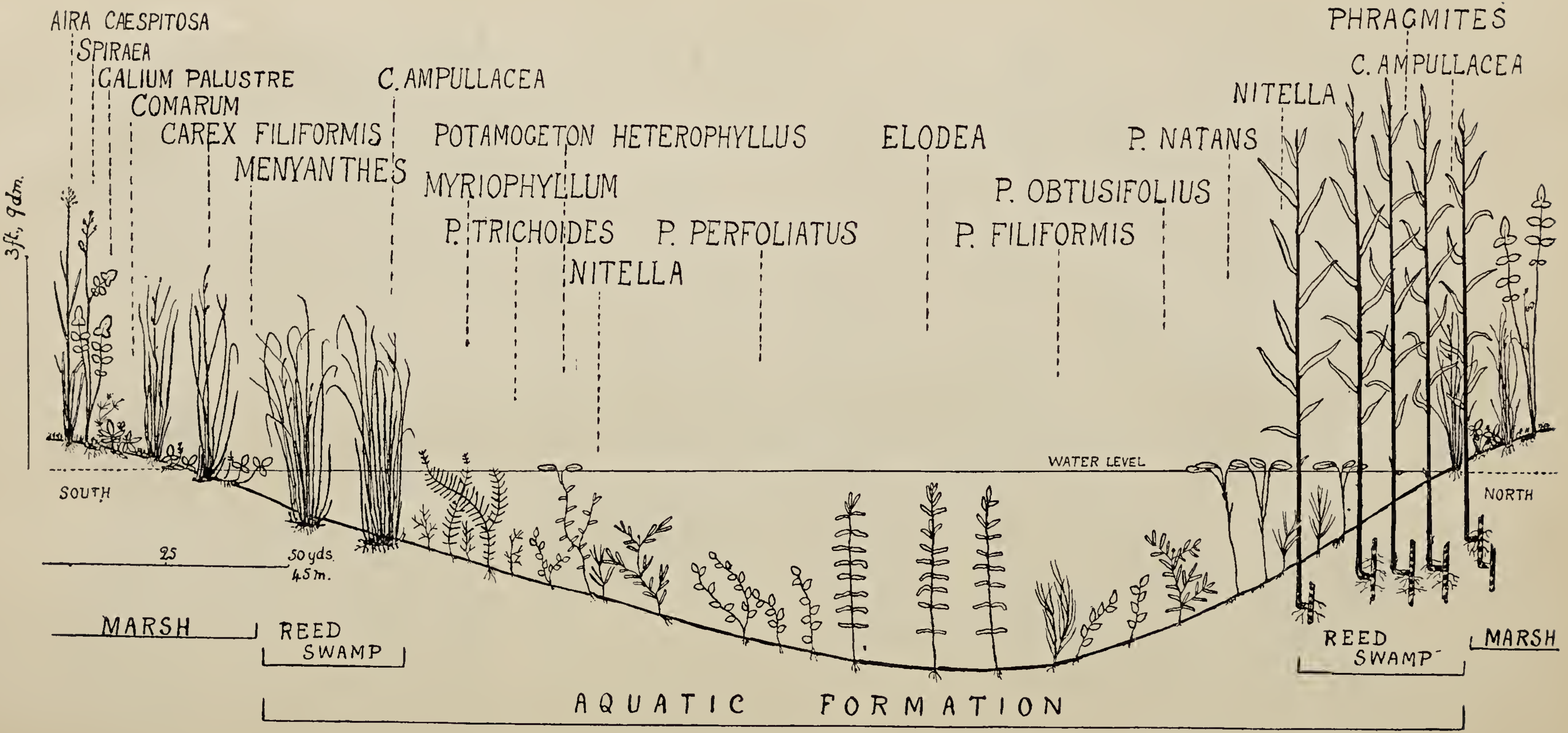


FIG. 2. Section along the line AB in Fig. 1, showing relations of plants to water environment. The trees of the marsh are not included. Vertical scale 1 : 36; horizontal scale 1 : 1550.

prevailing west to north-west wind by the tall reeds, and is covered so closely by the floating leaves of *Potamogeton natans* that few other species either floating or submerged occur. To the south and east sides the water is exposed to the wind, and on these sides broad-leaved floating plants are rare, their place being taken on the south side by *Myriophyllum spicatum.* This plant is adapted to wave motion, and its narrow leaves permit of considerable illumination of the bottom so that here a fairly dense lower storey of vegetation occurs. The accumulation of sand to about a foot in depth along the eastern side is due to wave action, and it is on this sandy bottom that *Chara aspera* var. *subinermis* forms a dense growth. Landwards, amongst the reeds on a similar substratum, *Litorella lacustris* is abundant. In such protected shallows Crampton found these species in the lochs of Caithness.[1]

In considering the reed-swamp it is difficult to say what has determined its distribution into the two communities already described. It is probably accidental that *Phragmites* does not occur on the south side, although the exposure of this side to wave action may have something to do with the absence of the plant. *Phragmites* is commonly absent from wave-beaten shores. It is only a few years ago, however, since the reed was confined entirely to the north side, but now the plants are extending round the eastern shore which is quite as much exposed as the south. In a short time they will undoubtedly meet the advancing extremity of the *Carex* consocies, for the distance which remains to be covered is small (see Map, Fig. 1). Already the zones have met at the west side and the dividing line between their extremities is remarkably distinct. Whether a struggle will occur between the reed and sedge, and whether the reed will ultimately establish itself right round the loch are interesting questions which time may determine. Meanwhile, both consocies are advancing inwards, and the struggle predicted may occur along a line from east to west now occupied by the open water.

In the herbaceous marsh a difference in the water-level separates the *Carex-Menyanthes* community from the *Comarum palustre* one, and alters their floristic composition.[2] "A change in the water-level very materially aids the plant dynamics in bringing about succession."[3] In the *Carex-Menyanthes* community, water to the depths of a few centimetres lies on the surface of the humus, and in this the bogbean flourishes. With the annual addition of sub-aqueous humus the surface of the substratum is raised, and the *Carex-Menyanthes* community becomes invaded by *Comarum.* The competition between the *Comarum* and the *Menyanthes* is really a struggle between two communities, and the result is the establishment of *Comarum palustre* to form what has been described as the *Comarum palustre* sub-association. Mosses now appear, the community becomes one in which the water-level is a little below the surface of the soil, and social species are much more abundant than in the *Carex-Menyanthes* community where the water-level is above the surface of the soil.

---

[1] C. B. Crampton. "The Vegetation of Caithness," 1911, p. 73.

[2] R. H. Yapp, *l.c.*, p. 72; E. Warming, "Ecology of Plants," 1909, p. 348.

[3] F. C. Gates, *l.c.*

The alder-willow association is confined to a fringe round the land margin where the accumulation of humus is greatest. As already mentioned, the trees have been planted, but the habitat is quite a natural one and the ground vegetation consists of typical marsh plants. Of these *Spirœa Ulmaria* is dominant, and at places is beginning to spread over the herbaceous marsh.

One outstanding feature regarding the vegetation of the White Moss compared with other similar habitats is the paucity of species. The plants of the highland loch—*Lobelia, Subularia,* and *Isoëtes*—do not occur, but it is more surprising that many lowland loch plants are also absent, *e.g.*, species of *Ranunculus, Nymphœa lutea, Castalia alba, Hippuris vulgaris, Epilobium hirsutum* and others.[1] *Nymphœa lutea* occurs in the back-waters of the Earn at no great distance from the loch. The writer is inclined to believe that the paucity of species is due indirectly to the raising of the humus level —the biotic factor which makes possible both the invasion of a community by the succeeding one and the centripetal encroachment of the vegetation as a whole—and directly to the actual suppression of the rarer species by those that are dominant in each successional stage. Competition as a biotic influence has already been mentioned in connection with the struggle between *Comarum* and *Menyanthes.* Other instances have come under the writer's observation where the competition has ended in complete suppression. Lindman[2] has given interesting examples of plants suppressed by other plants, and the cases which have been noticed at the White Moss may be cited.

About fifteen years ago an artificial curling pond was made near the S.E. corner of the loch (rectangular figure in map, Fig. 1).

---

[1] Cf. lists given for lowland lochs by R. and W. G. Smith, *l.c.*

[2] C. A. M. Lindman. "Some cases of plants suppressed by other plants." New Phytologist, Vol. 12, 1913, p. 1.

Water was introduced from the loch, but the pond failed to give satisfactory results and local curlers abandoned it. In a short time it became occupied by *Ranunculus aquatilis*, this species having spread from the loch. *Potamogeton natans* followed, became dominant in a few years, and the crowfoot ultimately disappeared. At the present time *Ranunculus aquatilis* is not found either in the pond or in the loch, but how it has been exterminated from the latter the writer is unable to say. Nor can definite reasons be given for the disappearance of *Utricularia vulgaris*, and *Zannichellia palustris*, both recorded in White's "Flora of Perthshire." The case of *Alisma plantago*, however, has been followed. Some years ago this plant was plentiful in the herbaceous marsh on the east side, but successional development accompanied by a dense growth of *Spiræa* has crowded it out, and the species is now represented by a single plant, which has taken refuge in a more aquatic habitat in the disused curling pond. In the herbaceous marsh on the west side *Triglochin palustre* occurred as an occasional species. It is now extinct, due to suppression by *Comarum palustre*. *Eleocharis acicularis* has entirely disappeared from the reed-swamp, and the same fate has befallen *Bidens cernua*.[1] Thus, in vegetational succession, in addition to the elimination of one community by another, there may be in the development of any one community a struggle between different species in which the subordinate are ultimately suppressed by the more potent.

THE PLANT SUCCESSION.

The developmental succession follows the order in which the plant-communities have been described, and in outline corresponds with the accounts given by other writers for similar habitats. Warming[2] gives a summary of the process for expanses of fresh water in Europe. Cooper,[3] in his detailed study of the vegetation of Isle Royale in Lake Superior, has described the development from aquatic vegetation to the final forest stage, and to the succession has applied the term *hydrarch*. The origin of the peat deposits in Ohio has been studied by Dachnowski,[4] who distinguishes five successions in the development of forest from an originally aquatic habitat. In Britain the succession has been noted by most writers usually when dealing with large areas. Miss Pallis[1] has described the succession from reed-swamp to fen associations, with which the marsh formation has a good deal in common. At the White Moss the initial stages are commenced when *Carex* on the one side and *Phragmites* on the other establish themselves in an advancing zone along the water-margin. The reed-swamp is an important transitional stage in the succession, for the accumulation of its organic débris prepares the way for the development of a new formation. Thus the series progresses from the aquatic formation to the ultimate development of a mesophytic community.

---

[1] J. R. Matthews, *l.c.*, p. 195.

[2] E. Warming, *l.c.*, p. 358.

[3] W. S. Cooper. "Vegetation of Isle Royale, Lake Superior." Bot. Gaz., Vol. 55, 1913.

[4] A. Dachnowski. "The peat deposits of Ohio." Review in Journ. of Ecol., Vol. I, 1913, p. 286.

In the process the part played by *Comarum palustre* is remarkable, for this plant succeeds equally well in its invasion of the preceding stage whether the soil is being formed on the one hand from the decayed plants of *Phragmites*, or on the other from the remains of *Carex* and *Menyanthes*.

CONCLUSION.

The "drying up" of the White Moss seems only a matter of time, for the centripetal encroachment of the marginal vegetation is fairly rapid. At one point on the south side where measurements have been made, the inward advance for the past ten years has been at the average rate of 1·3 m. per annum. But the rate of advance may vary from place to place. Along the eastern margin wave-action tends to obstruct the development of swamp vegetation, while its production goes on faster on the opposite side, which is towards the prevailing wind. Further, the slope of the substratum is gentlest from the west side of the loch, and this probably aids in the more rapid building up of the vegetation along this margin. As this development goes on the lake-stage will ultimately become extinct, and the first formation to remain stable will probably be marsh. But a few self-sown willow bushes have already appeared, and it is natural to conclude that in the course of time, an area will be presented completely devoid of open water but covered with a thicket of willow and elder.

In conclusion, the writer wishes to express his sincere thanks to Mr. Tansley for bringing to his notice the American publications mentioned on page 139 in which the term *consocies* is discussed in its new sense, and for much valuable criticism during the preparation of this paper.

---

[1] M. Pallis. "Fen Formation of East Norfolk," in "Types of British Vegetation," 1911, p. 230.

XEROPHYTIC ADAPTATIONS OF BRYOPHYTES IN RELATION TO HABITAT.

BY W. WATSON, B.SC.

[WITH THREE FIGURES IN THE TEXT.]

I. INTRODUCTION.

SOME years ago, when examining the bryophytes of the woodlands of Somersetshire (22), I was desirous of obtaining information on the characters which enable some species to live in dry situations, whilst others could only exist when provided with a large amount of shade or moisture. My search for information of this nature was only partially successful, as I could find no book or papers definitely dealing with it, but only scattered references to the subject in the works of Kerner (11), Goebel (7), Campbell (3), Haberlandt (9), Dixon (6), Warnstorf (19-21), Cavers (4, 5), Braithwaite (2), and others. Most of the required information had therefore to be gained from first-hand evidence by the study of the plants in the field and laboratory, and this paper is largely the result of such work, carried on for several years. A recent paper by Grebe (8) on the methods by which mosses protect themselves against drought, and an earlier series of articles by Wheldon (25), in which the xerophytic characters of some mosses were clearly shown and explained are of great value; these have been very useful to me in my later investigations, and extensively used in the arrangement of the matter for the present paper, which however deals with the liverworts as well as the mosses.

Every investigator of the distribution of bryophytes is aware of the difficulty experienced in dealing with these plants, especially with some mosses, because of their entirely different appearances in the moist or dry conditions. In order that he may identify them in the field, the bryologist must know them in both conditions, for the same species may be so entirely different in these two states that he may easily believe himself to be dealing with two different species. The habitat must also be clearly noted by all collectors of bryophytes, so that the species may be quickly and accurately named, since a knowledge of the habitat in which the plant actually occurs and the type of habitat from which the supposed species has been previously recorded may direct his attention to some easily-overlooked structural peculiarities known to occur in a plant of a certain habitat and not found in an otherwise similar plant from another habitat. Due care must be exercised in this respect, as a plant which is *normally* found in one habitat may *occasionally* be found in a quite different environment, and it is sometimes a matter of difficulty to decide to what species it actually belongs; thus a plant of half-shade may be a habitat-form derived from a shade plant, or it may be derived from a species which normally occurs in the open. This difficulty is often very real in dealing with species and their varieties; for example, *Alicularia Geoscyphus*, a liverwort of open ground, has a variety *suberecta* of shady or moist ground, and it is often impossible to refer a plant of half-shade either to the type or the variety, as characters pertaining to both may occur in it.

Edaphic factors, such as water-content, presence or absence of lime or other mineral substance, etc., often alter the appearance of the plant, and it is of interest to note that some mosses which have been discoloured by the urine of animals have had varietal names given to them. Here I may also mention an instance where the presence of a certain moss led me to examine the habitat more closely and definitely. I obtained a *Barbula* from a rock which appeared to be sandstone; on examination, the moss proved to be *B. tophacea*, a calciphilous species, and when the rock was tested with dilute acid the resulting effervescence distinctly showed the presence of a considerable amount of calcium carbonate. The occurrence of the moss thus proved to be a better test of the calcareous nature of the substratum, than perfunctory examination with the eye.

Amongst the bryophytes examples of hydrophytes, mesophytes and xerophytes are met with, but the ordinary meaning of the term mesophyte (as applied to the vascular plants) is quite inadequate when used for bryophytes. Various species which grow in habitats characteristic of phanerogamic mesophytes exhibit characters of a xerophytic nature chiefly because they have no roots which, penetrating to some depth in the soil, can obtain a constant water supply.

The hydrophytic ancestry of the bryophytes is clearly shown by the fact that they exhibit less complete structural adaptations to life on land than vascular plants do, but many of them are nevertheless able to live in habitats where they are cut off from a constant supply of water, though vigorous vegetative development and sexual reproduction can only be carried out when external water is available.

As the criteria of "mesophytism" in bryophytes are even vaguer than in vascular plants we must first obtain a clear conception as to what is really meant by xerophily in this group of plants. Warnstorf (20) considered the chief criterion for a xerophyte to be its dependence on atmospheric humidity, but Grebe (8) rightly criticises this definition, since it would include many mosses which grow on the bark and bases of trees in the shade of woods and yet are not xerophytes, because the atmospheric humidity is sufficiently great to allow the physiological functions to continue through a dry period. On the other hand, this definition would exclude a number of earth-mosses (some of which Warnstorf placed in a "semi-xerophytic" group (21)) which are truly xerophytic, and appear to be dead during a dry season. Grebe defines a xerophytic moss as one which is capable of surviving long periods of drought, is able to dispense with the soil-moisture, and at the same time shows some xerophytic structure (8).

During drought the vital activity of the plant may be suspended to such a degree that it appears to be dead, but when moistened it quickly revives and resumes its normal functions. Grebe's definition of xerophily in the bryophytes would embrace the inhabitants of exposed rock-surfaces (species of *Grimmia*, *Tortula*, *Weisia*, *Trichostomum*, *Encalypta*, *Gymnomitrium*, *Frullania*, *Lejeunea*, etc.), of dry heaths (e.g., *Polytrichum piliferum*, *P. juniperinum*, *P. gracile*, *Campylopus pyriformis*, *Rhacomitrium lanuginosum*, forms of *Gymnocolea inflata*), of dry banks or waste places (e.g., *Bryum argenteum*, *Weisia viridula*, *W. microstoma*), of trees growing in the open or in half-shade, as on trees with crowns which admit a good deal of light, such as the oak (e.g., *Ulota crispa*, *Orthotrichum diaphanum*, *Leucodon sciuroides*, *Grimmia Hartmani*, *Camptothecium sericeum*, *Cryphæa heteromalla*, *Frullania dilatata*, *F. Tamarisci*), and of dry sand-dunes (e.g., *Brachythecium albicans*, *Camptothecium lutescens*, *Scapania aspera*). It would include many plants which have their rhizoids fixed in the soil, whilst it would exclude some plants which are entirely dependent on atmospheric humidity, but which, owing to their enjoyment of constant shade, are kept sufficiently moist to continue their living activity through a period of dryness.

The cells of mosses are capable of withstanding long periods of drought or cold without being killed. This power is much more evident in bryophytes (and still more in lichens) than in the higher plants and may be considered to be a direct effect of life in dry or cold air rather than a xerophytic character. The same power is shown to a varying extent in higher organisms (17), and is correlated with the degree of interdependence amongst the cells, though modifications may be induced, either naturally or artificially, by altering the environment of the plant. The setæ of a moss grown in a damper atmosphere than its usual habitat are much sooner killed by drying than those produced under normal conditions. Irmscher has carried out many interesting and instructive experiments on drought and cold resistance in mosses; for details the reader may be referred to his paper (10).

A bryophyte which is capable of drying up without dying is therefore not necessarily a xerophyte; it must be able so to withstand long periods of dryness that sufficient cells are alive to enable the plant to resume its growth quickly when water becomes available, and to do this it must possess some of the xerophytic characters mentioned in the following pages.

Many small earth-mosses are annual species, their activity being only displayed in the moister half of the year, passing over during the drier portion as spores or underground protonema.

The chief protective arrangements against drought are shown in the gametophyte, which is usually perennial; the sporophyte has a much shorter life, especially in the Hepaticæ, its function being to produce and scatter the spores.

II. PROTECTIVE ARRANGEMENTS IN THE SPOROGONIUM.

During its development the sporogonium requires some protection, but when it is mature in the moss few protective devices are necessary, as it is built up of hard and firm tissue, the outer skin (exothecium) of the urn has its outer walls cuticularised, there is an intercellular space around the spore-sac, and the seta also has an epidermis of cuticularised cells. During the early days of the moss sporogonium its young and slender tissues are protected by the perichætial leaves of the gametophyte, and covered by the enlarged archegonial wall. When this wall bursts, the upper portion forms a bonnet (calyptra) which protects the unripe urn from dryness till its outer walls become cuticularised. In some mosses the perichætial leaves are much longer than the ordinary vegetative ones, e.g., *Seligeria pusilla*, *S. acutifolia*, *Archidium alternifolium*, species of *Pleuridium* (Fig. 1, 3, 4), *Eurynchium myurum*; in others they are convolute—e.g., *Barbula convoluta* (Fig. 1, 2), *Dicranella secunda*—or involute, e.g., *Dicranoweisia*, thus further protecting the young capsule; or they are fringed, as in *Diphyscium foliosum* (Fig. 1, 5) and *Thuidium tamariscinum*, the interlacing threads assisting by means of capillarity in the acquisition and retention of moisture.

The ripe sporogonium of the liverworts does not require so much protection as that of the mosses, since it is almost mature before the development of the seta, the rapid elongation of which can only occur during moist conditions. The capsule-wall is cuticularised and ringed fibres are sometimes present, but the seta is of a fragile and short-lived nature, quickly disappearing when the surroundings become drier. The capsule has no air-space, stomata, or columella, (except in the Authocerotales), the nutrition

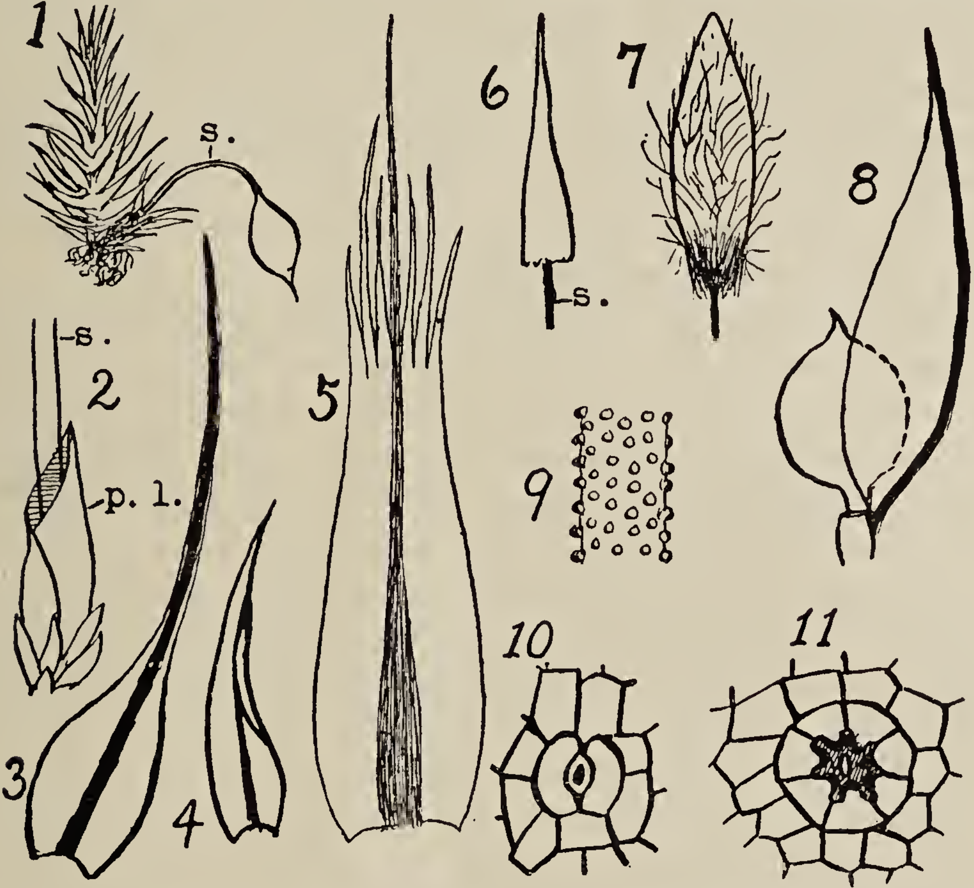


FIG. 1. Xerophytic Structures in Sporogonium of Mosses. 1, *Grimmia apocarpa*, showing curved seta (*s.*), × 4; 2, *Barbula convoluta*, showing perichætial leaves (*p. l.*) and ordinary leaves, × 16 (*s.*, seta of capsule); 3, perichætial leaf of *Pleuridium alternifolium*, × 16; 4, vegetative leaf of *P. alternifolium*, × 16; 5, ciliated perichætial leaf of *Diphyscium foliosum*, × 16; 6, calyptra of *Encalypta vulgaris*, × 4 (*s*, seta); 7, hairy calyptra of *Polytrichum piliferum*, × 4; 8, immersed capsule of *Physcomitrium pyriforme* (most of the perichætial leaves have been removed, only one being left), × 16; 9, papillose seta of *Brachythecium rutabulum*, × 160; 10, superficial stoma of *Orthotrichum affine*, × 320; 11, immersed stoma of *O. anomalum* v. *saxatilis*, × 320.

of the spore-sac depending almost entirely on the gametophyte. In the Jungermanniales, till the spores are mature, the capsule is enclosed by the calyptra and surrounded by more or less modified perichætial leaves, besides being usually surrounded by a special envelope (perianth) which begins as a ring at the base of the archegonial group, and keeps pace with the growth of the egg, though its production is generally independent of the occurrence of fertilisation. In some cases (e.g., *Cephalozia media*) the perianth is bistratose. In the Marchantiales the sporogonia are sunk in the archegonial cavity (e.g., *Riccia*) or the sporogonia are developed in heads (carpocephala) on the summits of bulky stalks belonging to the gametophyte, but usually developed after fertilisation, or even after the spores have matured. The involucral scales and hairs, the perigynium and the ventral position of the capsules are sufficient protection from dryness.

The special protective devices adopted by the sporogonium may be classed under the following heads.

(1) *Immersion of the Capsule* amongst the perichætial leaves, the seta being short or absent. This is often found in xerophytic mosses, and sometimes the perichætial leaves are much longer and finer-pointed than the vegetative leaves (e.g., *Archidium alternifolium*, *Pleuridium* spp., Fig. 1, *3*, *4*), or they may be ciliated (*Diphyscium foliosum*, Fig. 1, *5*) or convolute (*Acaulon muticum*). As examples of British plants may be mentioned *Cryphæa heteromalla*, *Hedwigia ciliata*, *Blindia cæspiticia*, *Physcomitrium pyriforme* (Fig. 1, *8*) and many species of *Orthotrichum*, *Grimmia*, *Phascum*, *Ephemerum*, *Andreæa*, *Neckera*, *Coscinodon* and *Weisia*.

(2) *The Length of the Seta* varies greatly according to the species and seems to be more or less independent of the habitat, as the greater length tends to ensure increased efficiency in spore-dispersal, but many species, which grow in dry situations have a form or variety of a damper habitat, and the seta of this is often longer than in the type. *Tortula muralis* is very variable in this respect, the var. *rupestris* of wet rocks, having a longer seta than the type, whilst the form of dry calcareous rocks has a shorter one; *Brachythecium velutinum*, when growing in moist or shady situations has longer setæ than when in a drier position.

(3) *Curvature of the Seta*, so that the capsule is wholly or partially sunk amongst the leaves of the gametophyte. When the spores are ripe, the seta more or less straightens out and the spores are dispersed, *e.g.*, many species of *Grimmia* (Fig. 1, *7*), *Campylopus*

spp. (fruit seldom found in the British Isles), *Dicranodontium longirostre, Campylostelium saxicola.*

(4) *Papillosity.* Thickenings of the epidermis so as to form protuberances are common in many organs associated with, or belonging to the sporophyte. The perianth is tuberculate or papillose in *Frullania dilatata* (Fig. 2, *16*), *Cololejeunea Rossettiana, Aplozia crenulata* var. *cristulata*, the calyptra in *Polytrichum aloides, Pottia asperula, P. Wilsoni, P. recta, Encalypta vulgaris*, etc., and the seta in *Brachythecium rutabulum* (Fig. 1, *9*), *B. velutinum, Buxbaumia* and some species of *Eurynchium.* Wheldon (25) throws doubt on the xerophytic character of the papillose seta in *B. rutabulum*, as he could find no relationship between the number and size of the papillæ to the various habitats of this species, but the general occurrence of papillæ on the leaves of xerophytes implies their xerophytic nature, and my observations on the influence of habitat on the length and papillosity of the setæ lead me to take a different view. It is quite probable that a comparative examination would not prove the papillose seta to be a xerophytic device, unless other disturbing factors were taken into account. In many mosses the exposed peristome is papillose (e.g., *Grimmia apocarpa*) whilst the spore is frequently ornamented with crests, ridges, or papillæ. Campbell says in regard to hepatics, after referring to the excrescences of the spore, "the exospore is especially well developed in species where the spores are exposed to great heat or dryness, ... in those species that are found in cooler and moister situations, the exospore is frequently thin" (3). This papillosity is shown in species of *Pottia, Gymnomitrium, Cololejeunea, Colurolejeunea, Fossombronia, Scapania*, in *Lophozia alpestris, Lepidozia reptans*, etc.

(5) *The bell-shaped calyptra* forms a protective bonnet over the urn in many species of *Encalypta*, (Fig. 1, *6*), *Funaria, Physcomitrium, Ulota, Orthotrichum.* It is hooded or cucullate in *Zygodon, Neckera, Seligeria, Grimmia crinita, Leptodon Smithii* and *Leucodon sciuroides.*

(6) The *Hairy Character of the Calyptra* and other protective bodies of the sporogonium, the hairs or cilia reducing transpiration and retaining water. The calyptra is hairy in *Polytrichum, Orthotrichum anomalum, O. leiocarpon, Encalypta ciliata, Leptodon Smithii*, etc.; the perianth is ciliate in *Chandonanthus setiformis, Lepidozia setacea, Lophozia guttulata*, and the perichætial leaves or bracts are finely pointed or ciliated in some xerophytic species of

mosses and liverworts, e.g., *Seligeria acutifolia*, *Chandonanthus setiformis*. The hairy vaginulæ of such mosses as *Orthotrichum stramineum* and *Leptodon Smithii* serve a similar purpose.

(7) The *Position of the Stomata*. When these are present, they are arranged in places where they are more or less shaded. In the smooth urns they are confined to the base of the capsule (e.g., *Orthotrichum leiocarpum*); in the grooved urns they are hidden in

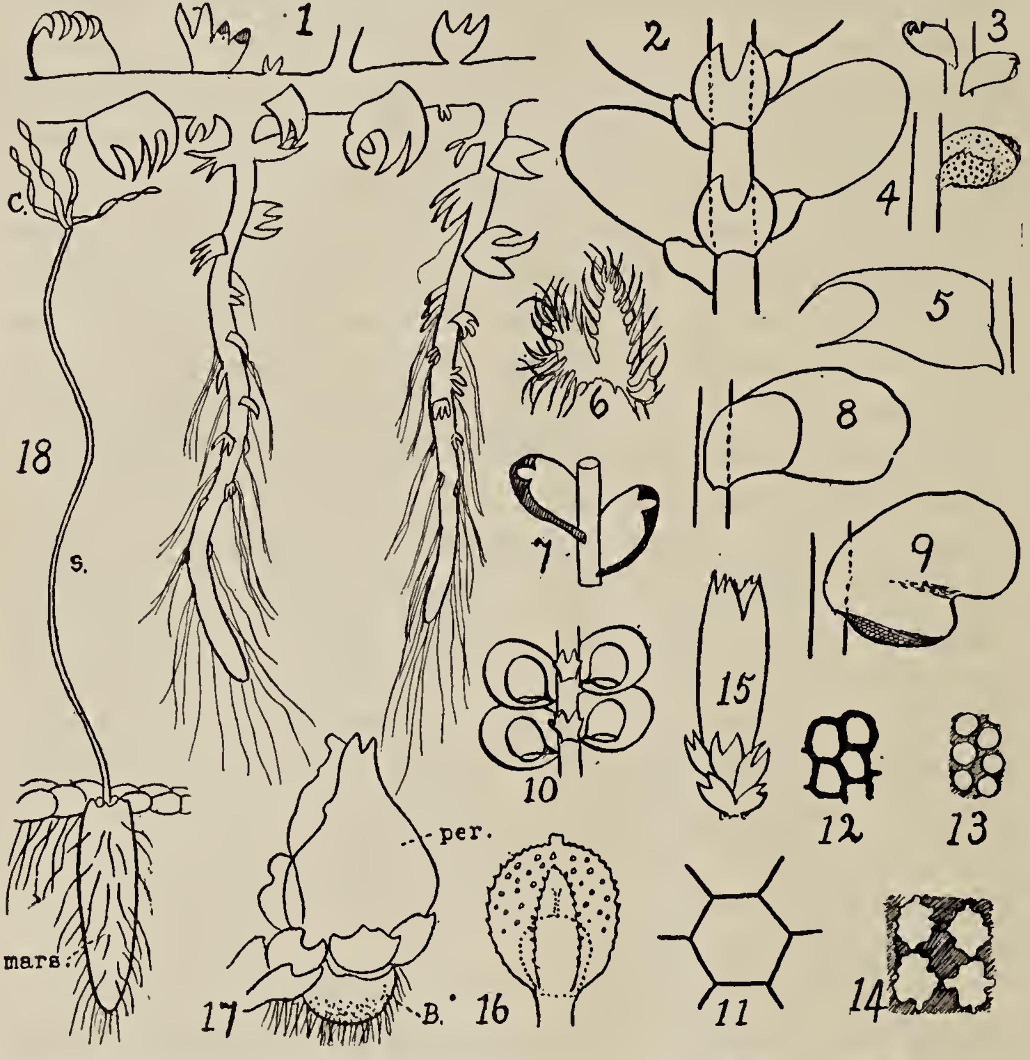


FIG. 2. Xerophytic Adaptations in Liverworts. 1, *Lepidozia reptans*, showing the leaves with incurved lobes, and two of the flagella, × 20; 2, *Lejeunea cavifolia*, shoot with water sacs and under-leaves, × 30; 3, stem and two leaves of *Lophozia atlantica*, showing the inturned apics of the three-lobed and concave leaf, × 10; 4, *Cololejeunea Rossettiana*, with papillose leaf, × 25; 5, stem and leaf of *Lophocolea cuspidata*, × 10; 6, ciliate leaf of *Ptilidium pulcherrimum*, × 10; 7, stem and two leaves of heath form of *Gymnocolea inflata*, × 10; 8, *Scapania undulata*, normal leaf, × 10; 9, *S. undulata*, leaf with diverging lobes, × 10; 10, *Frullania dilatata*, under surface showing water-sacs, × 10; 11, leaf-cells of *Chiloscyphus polyanthus* var. *fragilis*, a liverwort of wet places, × 200; 12, leaf-cells of *Alicularia Breidleri* with thick cell-walls, × 200; 13, leaf-cells of *Gymnomitrium adustum*, a liverwort of sub-alpine rocks, × 200; 14, leaf-cells of *Bazzania Pearsoni*, with very large trigones, × 200; 15, perianth of *Cephalozia media*, × 10; 16, *F. dilatata*, perianth with ridge and tubercles (position of sporogonium indicated by dotted lines), × 10; 17, bulbous involucre (B.) and perianth (*per.*) of *Alicularia Geoscyphus*, × 5; 18, marsupium (*mars.*) and sporogonium of *Calypogeia Trichomanis*, × 3 (*s.*, seta; *c.*, capsule valves).

the furrows (*e.g.*, species of *Orthotrichum* and *Ulota*), and the guard-cells may be sunk below the cuticular cells as in *O. anomalum* (Fig. 1, *11*) and *O. cupulatum*. In *Polytrichum piliferum* and its allies the stomata are found in the deep constriction between the apophysis and urn.

(8) *Plication of the Capsule* or the organs surrounding it, by means of which the assimilatory or protective surface is increased without a corresponding expansion of the exposed area. The calyptra is plicated in *Coscinodon cribrosus*, species of *Orthotrichum*, *Ulota crispa*, etc., the perichætial leaves in *Tortula ruraliformis*, and the perianth in *Chandonanthus setiformis*, and *Anastrepta orcadensis*. Striæ are often present in many xerophytic mosses (species of *Ceratodon*, *Orthotrichum*, *Encalypta*, *Cynodontium*, etc.) and these may partially serve a similar purpose, though the grooving is often only slightly evident before the maturity of the spores. In most cases the striæ are longitudinal but in some cases they are spiral, as in *Encalypta streptocarpa*.

(9) *Fleshy or bulbous involucre.* In *Alicularia Breidleri* and *A. Geoscyphus* (Fig. 2, *17*) the involucral base of the sporogonium forms a fleshy root-like body from which rhizoids penetrate into the soil. This "root" is really formed from the gametophytic tissue and forms a storehouse of food and moisture from which the foot of the sporogonium may draw its nourishment. That it is a xerophytic device is evident since it is absent or poorly developed in the moist or shady ground form (var. *suberecta*) of *A. Geoscyphus* In some plants, which can scarcely be considered as xerophytes, the involucre has extended still more, so that it forms a hollow tube (perigynium or marsupium) which is pendulous and more or less subterranean. This pendulous perigynium is found in *Geocalyx*, *Saccogyna*, and *Calypogeia* (Fig. 2, *18*) in all of which a perianth is absent.

In the somewhat hydrophytic *Riccia fluitans*, the capsule is enclosed in a spherical protuberance on the ventral side of the thallus and is furnished with rhizoids on the enclosing tissue.

III. PROTECTIVE ARRANGEMENTS IN THE GAMETOPHYTE.

The tissues are usually less resistant in the gametophyte than in the sporogonium, and the former has a longer life, so that some protection is necessary to ensure it against drying up. When water is present, it is quickly absorbed, and afterwards distributed to the various parts of the plant according to their requirements.

Many of the bryophytes exhibiting xerophytic devices are mountain or alpine plants (some of the *Andreæas* and *Grimmias* being found in the highest regions), but they are not limited to any altitude, seeing that they are present even at sea level, in fact, many of the plants growing on sand near the sea are essentially xerophytic, owing to the water derived from the substratum having a high osmotic value due to the large amount of dissolved salts.

Two general methods are adopted (A) the output of water is reduced, and this is the commoner method, or (B) some method of storing water is provided. Sometimes the same apparatus serves for both methods and will be considered under the first. As special protective devices the following may be given :—

A. REDUCTION OF WATER-OUTPUT.

(1) Cushion-forming Habit.

Many bryophytes grow in cushions or tufts, these being especially definite in such plants as *Grimmia pulvinata* and *Ulota crispa.* The interspaces between the leaves are markedly shortened, and the branches, when present, are closely crowded together. The cushion is capable of quickly absorbing water, and of retaining it for a much longer time than the free plant would be able to do, as only the apices of the leaves are exposed to evaporation. Everyone who is familiar with the tufted vascular plants knows how this character is increased in areas exposed to the wind, and the same thing is also true of these smaller plants. Under shadier, less exposed or damper conditions, the tufts are looser and higher, but when growing on exposed rocks or trees, they become compacter, so that not only is evaporation reduced, but they become more stable, since they offer a less area to be acted upon by the force of the wind.

Amongst tufted mosses growing on rocks, *Grimmia pulvinata, G. anodon, Trichostomum crispulum, T. nitidum, Orthotrichum anomalum, Encalypta vulgaris, Tortula muralis, T. ruralis, Barbula convoluta, B. revoluta,* offer excellent examples, the liverworts being represented by *Gymnomitrium obtusum, G. coralloides, G. alpinum, Sphenolobus saxicolus, Cololejeunea calcarea,* etc.

As tree representatives of this group may be mentioned *Zygodon viridissimus, Ulota crispa,* and *Dicranum montanum.*

Many mesophytic or hydrophytic plants have a form or variety of drier habitat which adopts this compact habit, enabling it to live in its drier position, e.g., *Ditrichum flexicaule* var. *densum, Bryum*

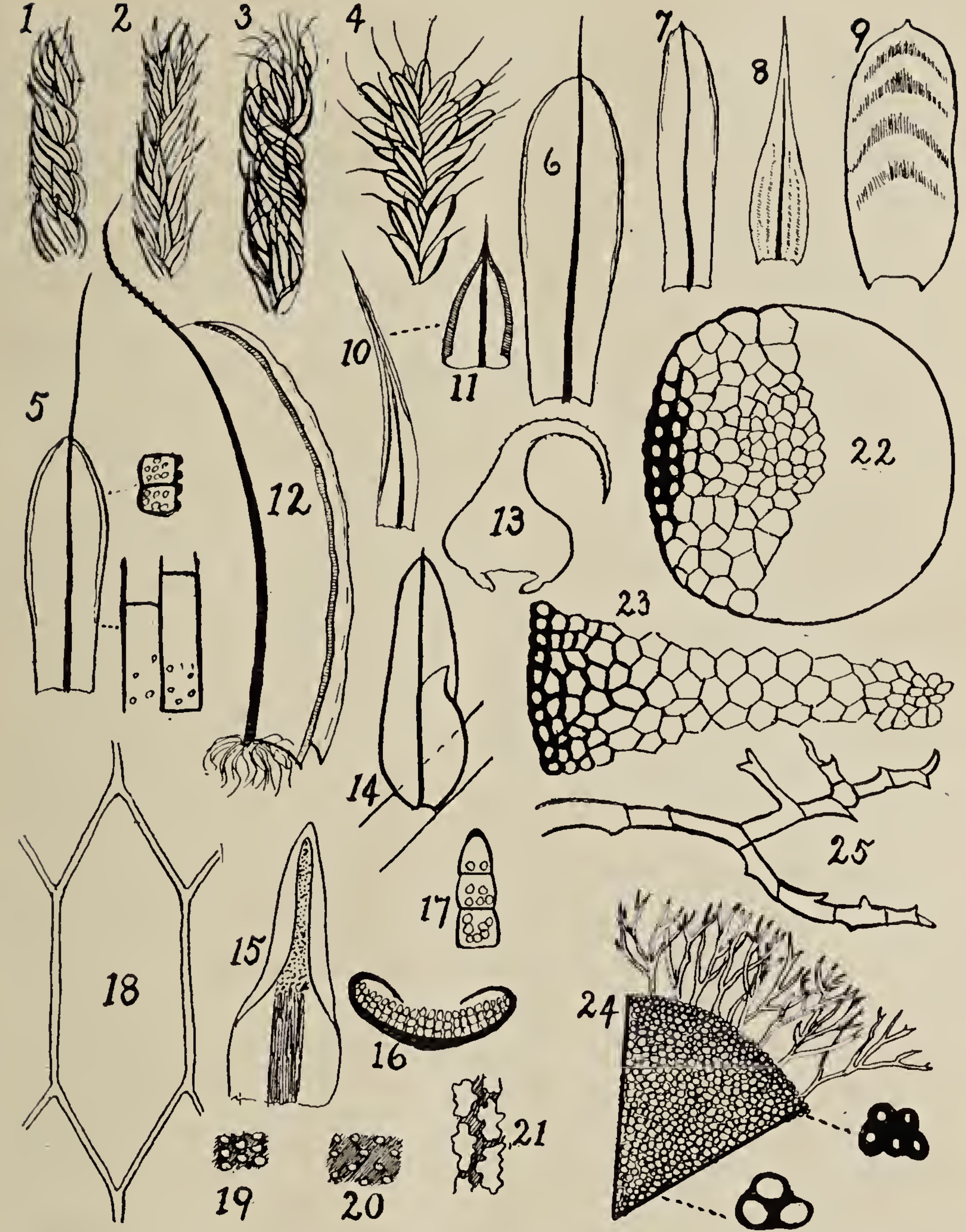


FIG. 3. Xerophytic Adaptations in Leaf and Stem of Mosses. 1, *Grimmia funalis*, dry condition, × 15; 2, *G. funalis*, moist condition, × 15; 3, *Tortula muralis*, leaves spirally twisted when dry, × 15; 4, *T. muralis*, moist condition, × 7; 5, *T. muralis*, leaf of normal plant, × 15, also papillose cells and cells of lower part of leaf; 6, *T. muralis* var. *rupestris*, of damper habitat, × 15; 7, *T. muralis*, leaf of plant from side of well, × 15; 8, plicate leaf of *Campothecium sericeum*, × 15; 9, undulate leaf of *Neckera crispa*, × 15; 10, leaf of *Weisia viridula*, with involute margin, × 15; 11, apical portion of same, × 70; 12, leaf of *Tortula ruralis*, showing the revolute margin and rhizoids at base, × 15; 13, falcate leaf of *Hypnum molluscum*, × 15; 14, leaf of *Fissidens taxifolius*, × 15; 15, cucullate leaf of *Tortula ambigua*, × 15; 16, section of same, showing inflexed margin and assimilating cells, × 45; 17, assimilating cells of same, with chloroplasts, × 150; 18, leaf-cells of *Pterygophyllum lucens*, a moss of moist situations, × 300; 19, leaf-cells of *Andreæa Rothii*, a moss of mountain rocks, × 300; 20, leaf-cells of *Ulota Hutchinsiæ*, a moss of siliceous rocks, × 300; 21, sinuose-walled cells of *Rhacomitrium canescens*, × 300; 22, transverse section of stem of *Leptobryum pyriforme*, showing the unequal thickening of the cortical cells (thick-walled on naked parts but thin-walled when shaded by the leaf-bases), × 200; 23, transverse section of stem of *Camptothecium sericeum*, × 200; 24, transverse section of stem of *Thuidium tamariscinum*, × 75, also outer and inner cells, × 300; 25, paraphyllium of same, × 300.

filiforme v. *juliforme*, *B. cæspiticium* v. *imbricatum*, *Weisia viridula* v. *densifolia*, *Cynodontium Wahlenbergii* v. *compactum* (on the higher Grampian rocks), *Fissidens adiantioides* v. *collinus*, *Polytrichum commune* v. *minus*, *Catharinea undulata* v. *minor*, *C. Crispa* v. *densifolia*, *Dicranella cerviculata* v. *pusilla*, *Dichodontium pellucidum* v. *compactum*, *Philonotis fontana* v. *compacta*, *Sphagnum cymbifolium* v. *congestum*, *S. papillosum* v. *confertum*, *Plagiochila asplenioides* v. *minor*, *P. punctata* v. *minuta*, *Gymnocolea inflata* form *compacta* (*f. laxa* and *f. natans* are lax forms of wet places), *Bazzania triangularis* (form of drier ground) *Madotheca rivularis* v. *faroensis*, *Cephalozia bicuspidata* v. *conferta*, *Lepidozia reptans* v. *julacea*.

(2) INVESTMENTS OF DEAD OR NON-CHLOROPHYLLOUS CELLS.

These protect the underlying chlorophyllous cells from too great evaporation.

(a) Hyaline Hairs or Hyaline Apices of the Leaves. These are especially characteristic of tufted bryophytes, which often have a white appearance in dry weather since the non-chlorophyllous cells are the only ones exposed. In this way the active chlorophyllous cells are screened from the drying action of the wind and from the too powerful rays of the sun. Hyaline hairs are present in many species of *Grimmia* (Fig. 3, *1*, *2*) *Rhacomitrium*, *Pottia*, *Tortula* (Fig. 3, *3-6*, *12*) *Campylopus*, *Bryum* and *Polytrichum*. They may be formed by the excurrent nerve as in *Tortula muralis*, *Pottia crinita*, *Bryum inclinatum*, and *Campylopus introflexus*, or simply by the apical cells of the finely-pointed leaves becoming non-chlorophyllous, as in *Hedwigia ciliata*, *Funaria calcarea*, *Hylocomium splendens*, *Coscinodon cribrosus*, *Eurynchium cirrosum*, *E. piliferum*, *Orthotrichum diaphanum*, and species of *Grimmia* and *Rhacomitrium*. The apex of the leaf is hyaline, but is not usually prolonged into a fine point in *Bryum argenteum*, *Grimmia apocarpa*, *G. torquata*, *G. elongata*, and in species of *Gymnomitrium*.

That this hyaline leaf-apex is a xerophytic arrangement is shown by the fact that many bryophytes displaying this peculiarity have varieties or forms of moister or shadier ground in which it is absent, whilst it is accentuated in forms of drier situations. The long hair-point is shorter or absent in forms of *Tortula muralis* growing on moist walls (Fig. 3, *6*, *7*), the var. *aestiva* of shaded rocks also having a short point. The hyaline points of *Grimmia apocarpa*, vars. *rivularis* and *gracilis*, *Rhacomitrium heterostichum* vars. *alopecurum* and *gracilescens*, *R. canescens* v. *ericoides*, are shortened or disappear entirely, and all these plants are found in moister or shadier situations than their types. On the other hand the grey tint due to the hairs is shown by drier ground forms of some mosses, in which the apical hyaline cells are not usually pronounced, e.g., *Phascum cuspidatum* v. *piliferum*, *Pottia bryoides* form *pilifera*, *Tortula pusilla* v. *incana*. *Bryum argenteum* when growing in very sunny situations has a longer point (var. *lanatum*), but when in damper places, its leaves are chlorophyllous almost to the apex (var. *majus*). *Hedwigia ciliata* also has two habitat-varieties, the hoary *leucophæa* of exposed positions, and the greener *viridis* of more shaded localities. In genera which usually possess these hairs, the more or less aquatic species are devoid of them (e.g., *Rhacomitrium aciculare*, *R. protensum*, *Grimmia atrata*, *Tortula mutica*), no water-plant has them, and they are usually absent in those mosses which are otherwise sufficiently provided for xerophytically, as in those with curly leaves (e.g., *Trichostomum*, *Weisia*).

Few liverworts possess hairs, but they are found on the thalli of *Metzgeria* and *Riccia*, especially in the dry ground forms. Amongst the foliose liverworts, the leaves of *Mastigophora* and *Ptilidium* (Fig. 2, *6*) are ciliate, and both these plants grow in dry spots, or in places which are liable to desiccation. In *Ptilidium* the species of drier ground (*P. pulcherrimum*) has the longer cilia, the plant of wet places (*P. ciliare* v. *inundatum*) having fewer and shorter ones.

(*b*) *Long-pointed Leaves*, with few chloroplasts in the apical cells act similarly to the hair-pointed leaves. The following xerophilous mosses have long-pointed leaves :—*Seligeria Doniana*, *Dicranella secunda*, *Dicranum falcatum*, *D. fuscescens*, *D. strictum*, *D. montanum*, *D. uncinatum*, *D. asperulum*, *D. longifolium*, *Orthodontium gracile*, *Neckera pumila* v. *Philippeana*, *Brachythecium glareosum*, *Ditrichum flexicaule*, etc. In *Hylocomium squarrosum* and to a less extent in *H. loreum*, the fine and paler tips of the squarrose-recurved leaves form the external portions of the shoots. Some liverworts display a similar principle in the lengthening of the leaf-lobes, e.g., *Lophocolea cuspidata* (Fig. 2, *5*).

(*c*) *Ventral Scales of Marchantiales.* During dryness the thallus of species of *Pressia*, *Reboulia*, *Targionia*, *Riccia*, etc., curves round so as to expose the non-chlorophyllous or slightly chlorophyllous ventral scales, which are often of a purplish colour. These scales cover over the incurved thallus, the chlorophyllous cells of which are not only protected by one or two layers of empty epidermal cells, but also by the scales as well, (*d*) *Protective Layer of Dead Cells*, with the chlorophyllous cells between them. In *Leucobryum*, a moss growing on heaths and turfy ground the chlorophyllous cells are covered except at the margin with two or more layers of rectangular hyaline cells whose internal walls are perforated with large pores, the internal chlorophyllous layer consisting of narrow and small cells, so that the plant has a whitish appearance. The presence of the pores renders absorption so easy that the moss may be said to suck up water like a sponge, and during dry weather, there is no doubt that the empty external cells act, not only as water-reservoirs, but also as screens against the warmth from the sun and the drying action of the wind. Goebel (7) describes a similar apparatus in the foreign moss *Syrrhopodon*. In the *Sphagna*, which are usually regarded as hydrophytic plants, and grow in bogs, we also get perforated hyaline cells, and it is significant that the plants growing in less "acidic" waters have greener leaves and fewer pores (e,g., *Sphagnum subsecundum* v. *viride*, *S. riparium*, *S. cuspidatum*).

(*e*) *Infolding of the Leaf-margins.* In *Polytrichum* spp. the wings of the leaves consist of hyaline cells and bend over the assimilating portion of the leaf (midrib) when the air is dry, so that only a small chink is left for the gas-exchange. This feature is specially marked in the species commonly found in dry or exposed places, e.g., *P. piliferum*, *P. sexangulare*, *P. juniperinum*.

(*f*) *Bordered Leaves.* Many species of mosses, have the margin of the leaf occupied by several rows of long empty cells, which not only serve as water-reservoirs, but also decrease the evaporating surface. These cells are the first to become desiccated, and then form a protective layer to the rest of the leaf, becoming more conspicuous during drying owing to the curling, crisping and curving of the leaf, thus acting as a screen to the underlying chlorophyllous cells. They are usually found in mesophytic plants with large cells, and compensate for the larger amount of transpiration that may take place owing to the size of the cell-cavities, e.g., *Funaria ericetorum*, *Tortula subulata*, *Webera Tozeri*, and some species of *Daltonia*, *Bryum*, *Mnium*, *Hookeria*, and *Sphagnum*.

Many mosses, which do not usually possess this character, often show narrower and less chlorophyllous cells at the leaf-margin, when they are growing in drier situations, e.g., *Physcomitrium pyriforme*, *Webera nutans*, *Funaria fascicularis*.

In the liverwort *Aplozia crenulata* the outer cells of the leaf-margin are larger and less chlorophyllous, and as forms which grow in water have this character absent or less pronounced, it may be considered a xerophytic device, especially as *A. crenulata* is the *Aplozia* most frequently found in dry situations, and has few other protective characters. The incurved margin of the leaf in *Odontoschisma Sphagni* is of a different nature, though it serves the same purpose. It usually consists of two layers of cells which are smaller and more incrassate than the central ones. This liverwort grows on *Sphagnum*, but the bog-moss is often more or less decayed, and the habitat may be a fairly dry one. *Riccia sorocarpa* also has thick-walled epidermal cells.

(3) THE SHAPE OF THE LEAF OR THALLUS.

(*a*) *Involute Leaves.* The upper portion of the leaf is incurved, the margins being rolled inwards to form a kind of tube, so that evaporation is reduced. *Weisia crispa, W. crispata, W. viridula* (Fig. 3, *10, 11*), *W. tortilis, Dicranodontium longirostre, Dicranum scoparium* v. *spadiceum, Tortula papillosum* show this character.

(*b*) *Cucullate Leaves.* The apex of the leaf is inbent to form a hood enclosing a cavity, the assimilating area remaining the same whilst evaporation is reduced, e.g., *Tortula brevirostris, T. ambigua* (Fig. 3, *15*), *T. aloides, Polytrichum sexangulare, Trichostomum crispulum, T. inclinatum, T. flavovirens, Encalypta streptocarpa, Grimmia unicolor, Webera cucullata, Cylindrothecium concinnum.*

The inturned apices of the leaf-lobes of *Lophozia atlantica* (Fig. 2, *3*), *Gymnomitrium alpinum, Colurolejeunea calyptrifolia, Cephalozia bicuspidata* v. *conferta, Alicularia Breidleri, Lepidozia reptans* (Fig. 2, *1*), *Anastrophyllum Donianum, Gymnocolea inflata* f. *nigricans* (Fig. 2, *7*) and some other liverworts answer the same purpose.

(*c*) *Revolute leaves.* The margin is bent backwards in *Tortula muralis, T. ruralis* (Fig. 3, *12*), *T. intermedia, Barbula revoluta, B. Hornschuchiana, B. gracilis,* and some other xerophytic mosses (species of *Grimmia, Orthotrichum* and *Bryum*).

(*d*) *The Concave Leaf.* The boat-like leaf not only reduces the evaporation whilst maintaining its photosynthetic standard, but also provides a chamber which holds moisture, moreover the water-holding power is increased by the close approximation of the leaves. The concave leaf is very common amongst the bryophytes, and may be especially noticed in *Bryum argenteum, B. capillare* v. *elegans, Brachythecium purum, B. illecebrum, B. cæspitosum, Eurynchium crassinervium, E. piliferum, E. circinatum, E. murale* v. *julaceum,* *E. myurum*, *Sphenolobus minutus*, *Lophozia bicrenata*, *L. confertifolia*, *Cephalozia bicuspidata* v. *conferta*, and in the alpine *E. cirrosum*, *S. saxicolus*, *Pleuroclada albescens*, *Marsupella condensata*, *M. apiculata*, *Gymnomitrium* spp., and *Odontoschisma Macounii*.

(*e*) *Undulate Leaves*. The reduction of the transpiring surface is accomplished by the lamina being transversely folded, thus forming a number of small chambers in which the water can be retained. They are beautifully shown in species of *Neckera* (Fig. 3, *9*), as well as in *Dicranum undulatum*, *D. spurium*, and *Plagiothecium undulatum*. On dry heaths *Hylocomium triquetrum*, *H. splendens*, *Dicranum scoparium* and some other non-undulate species of mosses, are often found with undulate leaves. In *H. rugosum* and *Dicranum Bonjeani* v. *rugifolium* the small chambers are more of the nature of little pockets than transverse folds. The wavy nature of some liverworts has a similar purpose, e.g., *Petalophyllum Ralfsii*, *Alicularia Geoscyphus*, *Lophozia incisa*, and dry ground forms of *L. Floerkii*.

(*f*) *Plicate Leaves*, in which the folds are arranged longitudinally may serve for strengthening purposes, but the main use of the plication seems to be for protection against dryness. This form of leaf is found in *Camptothecium sericeum* (Fig. 3, *8*), *C. lutescens*, *Leucodon sciuroides*, *Brachythecium plicatum*, *B. albicans*, *Eurynchium strigosum*, *E. striatum*, *Ptychomitrium polyphyllum*, *Breutelia arcuata*, and species of *Thuidium* and *Hylocomium*. It is commoner amongst the pleurocarpous than the acrocarpous mosses, and as Grebe (8) notes, mosses with plicate or undulate leaves have few other protective arrangements, the cells are poor in chlorophyll, and the cell-membranes are firm and tough. Plicae are present in some apparent hydrophytes as *Hypnum uncinatum* and *Climacium dendroides*, but even these are able to suffer dryness, as I have found them in such dry places as on Carboniferous Limestone heathy pasture. It is also to be noted that some forms or varieties of such plants, growing in water poor in osmotic substances, have the leaves less plicate than the type, e.g., vars. *falcatum* and *virescens* of *Hypnum falcatum*.

4. THE SIZE OF THE LEAF-CELLS.

The cells are usually smaller in xerophytic bryophytes, but not always so, since other adaptive characters must be taken into account; it is, however, the rule in comparing two or more species of the same genus, to find the smaller-celled one to be a plant of drier habitat. The large-celled mosses, *Pterygophyllum lucens*

(Fig. 3, *18*), *Mnium subglobosum*, *Cinclidium stygium*, are found in wet or shaded situations, whilst exposed Alpine plants (species of *Andreæa*, *Grimmia*, and *Leskea*) have small cells with thick walls (Fig. 3, *19-21*).

In the Hepaticæ, which are a more hydrophilous class than the Musci, we usually find much larger cells (Fig. 2, *11*), though some xerophilous liverworts have relatively small ones, e.g., *Anastrepta orcadensis*, *chandonanthus setiformis*, *Bazzania triangularis*, and species of *Gymnomitrium* (Fig. 3, *12-14*).

Mosses with nerveless leaves often have long cells so that conduction can take place in a longitudinal direction more readily.

(5). THICKENINGS OF THE LEAF-CELLS.

These thickenings not only strengthen the leaf, but at the same time, decrease the transpiring surface.

(a) Papillosity. The papillosity of the leaf is the most important adaptive character of a structural nature in the mosses. The papillæ arise as local thickenings of the cell-wall and appear as small warts on the surface of the leaf. They are found in many xerophytes, sometimes being so numerous that the cells are completely hidden beneath them, but in some families (e.g., Grimmiaceæ) they are almost entirely absent, as these mosses are sufficiently provided for in other ways. They are found in *Hedwigia ciliata*, *Rhacomitrium canescens*, *Pseudoleskea catenulata*, *Myurella julacea* v. *scabrifolia*, *Pterigynandrium filiforme* and many species of *Barbula*, *Tortula*, *Encalypta*, *Trichostomum*, *Weisia*, *Zygodon*, *Anomodon*, *Leskea* and *Thuidium*. Under moist conditions some mosses which have papillose leaves become almost smooth. I have noticed this especially in *Barbula fallax*.

Mammillæ appear to be of a similar nature, but instead of being solid structures are only vesicular. They are present in *Timmia* and *Philonotis*, and Grebe (8) considers them to correspond to gemmæ, though he gives no evidence in proof of this.

Some liverworts also have their leaves studded with similar small warts, e.g., *Cololejunea Rossettiana*, *C. calcarea*, *Scapania aspera* *S. nimbosa*, *S. æquiloba*.

(b) Incrassate "Cell-nets." The walls of the leaf-cells are often thickened so that they offer a greater resistance to desiccation. This peculiarity is seen in the leaves of xerophilous species of *Andreæa*, *Zygodon*, *Orthotrichum*, *Barbula*, *Tortula*, *Rhacomitrium*, *Grimmia*, *Ulota* (especially *U*, *Hutchinsiæ*), *Weisia*, etc., all of which have very small cells, less than 5 μ in diameter and usually cubical

or spherical in shape. The thickening is often more apparent at the edges of the leaf, as in *Orthotrichum diaphanum*, etc.

In *Rhacomitrium*, *Andreæa petrophila*, *Jamesoniella Carringtonii*, *Anastrophyllum Donianum*, and some species of *Grimmia*, the cells are sinuose, so that the absorbing and conducting surface is increased, as in the cells of *Pinus*, thus compensating for the greater difficulty in conduction owing to reduction of cell-diameter and increase in thickness of cell-wall.

The cell-walls are also thickened in the liverworts *Alicularia Breidleri*, *Lophozia alpestris*, *L. bicrenata*, *Sphenolobus minutus*, *Diplophyllum albicans* and species of *Gymnomitrium*, but usually this thickening is more conspicuous at the angles so that triangular masses (trigones) appear to be present between the cells as in *J. Carringtonii*, *A. Donianum*, *L. porphryoleuca*, *S. saxicolus*, *Plagiochila punctata* v. *minuta*, *Chandonanthus setiformis*, *Bazzania triangularis*, and in species of *Targionia* (epidermal cells), *Frullania* and *Ptilidium*. The presence of trigones seems to be quite as characteristic a xerophytic adaption for the liverworts as the occurrence of papillæ in the mosses.

The cells of most bryophytes have their greatest diameter across their middle portions, so that their superficial walls may be said to overlap their respective cells.

(c) Doubling of the Lamina is a xerophytic device, which acts in a similar manner, but is of uncommon occurrence. Sometimes the entire lamina is doubled, but usually the thickening is confined to the margins of the upper portion, which is most likely to be exposed during drying. This bistratose character of the margin is found in *Coscinodon*, *Campylostelium*, *Tortula marginata*, *T. angustata*, *Orthotrichum rupestre*, *Bryum Donianum*, and many species of *Grimmia*. It is also present in some hydrophilous mosses (e.g., *Cinclidotus*) and then serves to protect the leaf from injury (25).

The sclerotic cells scattered in the thallus of *Preissia* appear to be chiefly concerned in giving rigidity to the plant.

(d) Midrib. The thickening and widening of the midrib, and consequent reduction of the lamina is of common occurrence in xerophilous mosses, the strong fibrous leaf being more resistant to drought. This structure is found in *Andreæa crassinervia* *Dicranella heteromalla*, *Dicranodontium longirostre*, *Dicranum longifolium*, *D. asperulum*, *D. uncinatum*, species of *Diphyscium*, *Swartzia*, *Polytrichum*, *Seligeria*, and *Campylopus*. In *Polytrichum* the surface

of the midrib is covered by vertical plates of chlorophyllous cells, which compensate for the reduction of the ordinary assimilatory tissue, and these may be protected by having the row of cells terminating each plate widened (*P. commune*) or papillose (*P. alpinum*, *P. urnigerum*) or almost without chlorophyll. A form of the dry heath-loving *P. gracile* found in a damp locality had the lamminæ so much larger, and the lamellæ so much reduced, that it was originally described as a new species of Catharinea (*C. Dixoni*). Goebel (7) notes the fact that if *Polytrichum* be cultivated in water the old leaves blacken and die, whilst the new leaves have less tall lamellæ. A similar method of compensation for reduced leaf-surface is found is some species of *Tortula* (Fig. 3, *15-17*).

The presence of a nerve may in some sense be considered a character of a xerophytic nature, since as Haberlandt showed (9) it occurs in mosses inhabiting soil and is related to water conduction. The leaves of leafy liverworts are generally without midribs, the only foliose British species showing any sign of a midrib being *Diplophyllum albicans*, but this does not appear to be directly related to water conduction (Tansley and Chick, 18).

(6). STEM STRUCTURE.

There is comparatively little differentiation of the stem-cells in bryophytes, the central strand being the only indication of vascular tissue, and this seems to bear little relationship to xerophily, but is rather related to whether the plant lives on soil or not (Haberlandt, 9). Where conduction is provided for by external capillary means, it is reduced or entirely absent, e.g., *Thuidium*. In *Polytrichales* there is some differentiation between the water-conducting and the other cells of the central strand (18), in the central strand is usually present, in Andreæales it is absent, in Hepaticæ it is absent or rudimentary. The cortical cells appear to have some relationship to the habitat, but even here no very definite statement can be made as to the amount of thickening which takes place, since it is modified by the degree to which the stem is exposed. Generally, it may be said, that a xerophilous bryophyte has a cortex of cells with thickened walls, whilst a plant of a moist habitat has a cortex of thinner and larger cells. In many mosses where parts of the stem are exposed, whilst other parts are covered by the leaf-bases, the cortical cells of the former are more incrassate and smaller than those of the latter.

(7). ARRANGEMENT OF THE LEAVES ON THE STEM.

This is one of the most important methods of protection against dryness. During moist conditions the leaves quickly absorb water and open out; with a drier environment, they place themselves close to the stem, or inroll, or curl, or display some other movement which makes the surface of evaporation less. The leaves which perform these movements have larger and less chlorophyllous cells at the base; these are often provided with small pores, are more active in absorbing and losing moisture than the upper leaf-cells, so that their expansions and contractions may be regarded as the causes of leaf-movement.

The following are the main changes in form and position of the leaves during the changes in humidity.

(a) Imbrication of the Leaves in the Dry State. The leaves, on the approach of dryness, lay themselves on the stem, so as to fit closely together like the tiles of a house, the chief parts exposed being the upper portions (which are sometimes hyaline), the thick nerve, or the revolute margins. This method is very common amongst the mosses, being well shown in many species of *Bryum* (especially *B. cæspiticium* v. *imbricatum*, *B. argenteum* and *B. provinciale*), *Grimmia*, *Rhacomitrium*, *Polytrichum*, *Andreæa*, *Pseudoleskea*, *Myurella*, in *Ulota Hutchinsiæ*, *Hedwigia imberbis*, *Barbula fallax*, *Leucodon sciuroides*, *Leskea nervosa*, *Brachythecium albicans*, and *Camptothecium sericeum*. It is also met with amongst the liverworts as in *Aplozia crenulata*, *Chandonanthus setiformis*, *Lophozia bicrenata*, *Madotheca platyphylla*, *Plagiochila punctata* v. *minuta*, *P. asplenioides* v. *minor*, *Cephalozia bicuspidata* v. *conferta*, *Gymnomitrium* spp., and other plants of dry ground. In *Aplozia crenulata* and *Odontoschisma Sphagni* the chief parts exposed are the thickened cells of the leaf-margin.

(*b*) *Spiral Twisting of Leaves in the dry State.* The drying leaves are not only in opposition to the stem and to each other, but are also spirally twisted round the stem, so that their apices and nerves are the chief portions exposed. This is a more efficient method than mere imbrication, in a greater or less degree is common amongst the acrocarpous mosses, and is well shown in *Tortula muralis*, *T. ruralis*, *T. lævipila*, *Barbula revoluta*, *B. Hornschuchiana*, *B. convoluta*, *B. unguiculata*, *Trichostomum fragile*, *Grimmia funalis*, and *Encalypta vulgaris*. In *Bryum capillare* the leaves are usually strongly spirally twisted, but in the variety *flaccidum* of moist sheltered situations, they are more distant and are neither spirally twisted nor appressed. In *B. Donianum*, an allied plant, and usually quite as xerophilous, the spiral twisting is not very pronounced, the thickened cells of the border rendering such a process unnecessary. *Tortula ambigua* seldom has this spiral twisting but it is often present in wall-side specimens.

The spiral twisting of the peristome in *Barbula* and *Tortula* has also a similar use for the protection of the teeth in the sporophyte.

(*c*) *Curving or Curling of the Leaves in the Dry State* is another method which is similar to spiral twisting, in fact the two processes are somewhat similar. It is found in *Ulota crispa*, *Barbula cylindrica*, *B. sinuosa*, *Pleurochæte squarrosa*, *Weisia crispa*, *W. sterilis*, *Cynodontium Wahlenbergii*, *Dicranoweisia*, *Dicranum montanum*, and especially in *Trichostomum crispulum*, *T. mutabile*, *T. flavovirens*, *T. nitidum* and *T. tortuosum*, all of which have leaves which are circinate, or so strongly curved as to be spirally inrolled on themselves.

(*d*) *Slighter Variations on Drying*, so that the leaves are less exposed, are present in many xerophytic bryophytes which do not possess any of the above-mentioned methods to a pronounced degree. They are also found in many plants which are mesophytex, or at the most, can only be considered semi-xerophytes. These variations include such changes as the crisping of the leaves in *Diphyscium foliosum*, *Anomodon viriculosus*, *Dicranum fuscescens*, *Encalypta streptocarpa*, the crumpling (or leaves becoming flexuose) in *Campylopus flexuosus*, *Barbula rubella*, *Dicranum fulvellum*, and many pleurocarpous mosses and foliose liverworts, e.g., *Lophozia Flœrkii*.

(*to be continued*).

NOTES ON RECENT LITERATURE.

CHONDRIOSOMES (MITOCHONDRIA) AND THEIR SIGNIFICANCE.

By F. Cavers.

(continued from p. 106).

Criticisms of the Chondriosome Origin of Chromatophores.

WE have seen that the work of Lewitsky and of Pensa, and later that of Forenbacher and of Guillermond, led these writers to conclude that chromatophores (leucoplasts, chloroplasts, chromoplasts) in flowering plants arise by morphological and chemical processes of transformation from chondriosomes which are homologous with those described for animal cells and which in turn arise by division of pre-existing chondriosomes in the cells of embryonic tissues and may be traced back to the oosphere itself. Since this conclusion is, at first glance at least, violently opposed to the view associated with the names of Schimper and Meyer—that chromatophores always arise by division of pre-existent chromatophores—it is natural that it should not long go unchallenged. Meyer (1911) criticised Lewitsky's work on various grounds, though his criticism strikes one as consisting mainly in a refusal to believe that anything new remains to be discovered in vegetable cytology and a declaration that the last word regarding the development of chromatophores was said by himself and Schimper about thirty years ago. Meyer pointed out that if the Lewitsky-Pensa view is correct we have a discovery of something entirely new in the plant cell, in which hitherto there have been distinguished (1) protoplastic structures which alone multiply by division, namely, the nucleus and the chromatophores (2) alloplasmatic structures which arise by alteration of the normal cytoplasm, such as flagella, hautschicht, vacuolar membranes, and (3) ergastic structures which arise *de novo*, such as starch grains and calcium oxalate crystals; to these must now be added, according to Pensa and Lewitsky, (4) chromatophores which arise from special cell-organs not belonging to the normal cytoplasm and differing morphologically and physiologically from the chromatophores themselves. He also claimed that there is no special method of staining which will distinguish any one kind of protoplasmatic or alloplasmatic structure from another, and that conversely the same stain reaction may be given by totally different cell structures, hence we have no right to assume that all structures stained by the Benda-Meves method are necessarily morphologically and physiologically similar. Finally he demanded more definite proofs that chondriosomes can be distinguished from small chromatophores and that the actual transformation of the former into the latter can be actually seen directly in the living cell, as for instance in filamentous Algæ.

Schmidt (1912) published a general review of work on plant chondriosomes up to November, 1911, which he supplemented by a further review (1912) including 1911 and 1912 papers by Lewitsky, Forenbacher and Guillermond. In the general (Progr. rei bot.) review—useful, though incomplete and somewhat misleading—he showed strong bias in favour of the Schimper-Meyer theory and entirely overlooked a considerable body of work done during recent years which has either thrown considerable doubt upon the universal application of that theory or has altogether disproved it in the case of flowering plants at any rate (see general discussion later on the origin of chromatophores). In the second review he somewhat distorts Guillermond's views, and attempts to turn the table upon the advocates of the view that chromatophores arise from chrondriosomes, by stating that the work of Lewitsky, Pensa, Forenbacher and Guillermond simply confirms the Schimper-Meyer view—according to Schmidt, these workers were merely dealing with the very early stages in the development of plastids which their technique enabled them to observe and which the simpler methods used by Schimper and Meyer were inadequate to demonstrate. According to Schmidt there are three possible interpretations of the nature of plant chondriosomes: these bodies are either (1) chromidia corresponding to those of animals, that is, portions of chromatic material derived from the nucleus, or (2) chromatophores in early stages of growth, or (3) special cytoplasmic structures. With regard to the first, he points out that very few botanists support the view that plant chondriosomes are actually extruded nuclear chromatin bodies, and that this view can only be accepted when confirmed by observations on living material; as to the second, that chromatophores in all stages of development give the same staining reactions as those considered characteristic for chondriosomes, and that (as stated above) in his opinion the new workers have simply brought valuable support to the Schimper-Meyer view; while he denies altogether the probability or possibility of the third view. However, for the greater part, Schmidt's criticisms are practically repetitions of those made by Meyer and referred to above, but though he appears to do less than justice to Lewitsky's careful investigations it must be admitted that there is, as he points out, much room for further work on this subject and on that of plant chondriosomes generally.

Rudolph (1912) published the results of his investigations in which he used the same plant *(Asparagus officinalis)* as that on which Lewitsky's earlier work was mainly done. His object was to ascertain the relation of chloroplasts to chondriosomes, and he examined only the shoot-tip. On the whole his observations agree with those of Lewitsky as regards the chondriosomes themselves, but he could find no evidence of any relation between these bodies and the chloroplasts, and indeed he ends his paper with the remark that the single established fact resulting from all the work hitherto done on plant chondriosomes is that of the existence of such bodies in a large number of plants belonging to various groups. He found that in the youngest meristem cells the only chondriosome-like bodies present were granular, and that filamentous forms made their appearance later and were evidently produced by elongation of the granules prior to their division, Some of the granules in these young cells grew rapidly and gave rise to chromatophores, while the remainder retained their original size or produced longer or shorter filaments arising by incomplete separation of the divided grains; and as these unaltered bodies were found along with chromatophores in fully developed cells, he attempts to draw a sharp distinction between the two kinds and elaborates the view that chromatophores and chondriosomes are structures of entirely different nature and that there is no genetic connexion between them. He admits, however, that though he could find no transitional forms such as those described by Pensa, Lewitsky, Forenbacher and Guillermond, he could on the other hand detect no differences between those granules in the meristematic cells which by continued division gave rise to the numerous chondriosomes found in older cells and the granules which on his view give rise to the chromatophores; yet he concludes that these primary granules are of quite different nature and supports the Schimper-Meyer view of the origin of chromatophores from pre-existing chromatophores. This strange piece of reasoning is backed up by the argument that if Lewitsky's view be adopted we have a sharp break in the phylogenetic series: it is admitted that in Algæ with a single large or primitively constructed chromatophore the latter is invariably derived by division from that of the parent cell or cœnocyte, while according to Sapehin (see below) all the chloroplasts in a Moss plant are derived by division from the single chromatophore present in the spore, hence it is *prima facie* improbable that the chromatophores in higher plants should originate in a different manner. Rudolph examined a number of Algæ, Fungi and Mosses, also *Selaginella*, but could find no chondriosomes in any except *Achlya* and *Vaucheria*. He gives citations of a number of papers in which earlier authors described chondriosome-like structures in various groups of flowerless plants, but points out that further investigation of these bodies is required.

Sapehin (1911) observed during a study of sporogenesis in Mosses that each archesporial cell contained one or two deeply staining bodies, often lying close to the nucleus, and on tracing the fate of these bodies in both fixed and fresh material found that they were not centrospheres but chloroplasts. He examined various other plants and found that one or a pair of plastids occurred in the archesporial cells of *Anthoceros*, all the Mosses investigated, *Selaginella* and *Isoëtes*, while in the remaining Hepaticæ and Pteridophytes, as also in the Spermophytes, the archesporial cells contained each a considerable number of plastids. The single chloroplast of the *Anthoceros* spore-mother-cell and its division had, of course, long been known. Sapehin traced the division of the single chloroplast in the spore-mother-cell of various Mosses into four, one going into each spore of the tetrad, and found that this divided repeatedly so that the ripe spore contained several chloroplasts, as did all the cells of the gametophyte and of the embryo sporophyte. The reduction in number of the plastids to one in the spore-mother-cell takes place simply by the division of the chloroplasts ceasing to keep pace with that of the nucleus in the cells of the sporogenous tissue (spore-sac), so that eventually each archesporial cell contains only one or sometimes two. In a second paper Sapehin (1913) noted that *Lycopodium* is to be added to *Selaginella* and *Isoëtes* as a third Pteridophyte in which the archesporial cell contains a single plastid. He found that in *Funaria* the behaviour of the plastids in gametogenesis exactly resembled that previously described by him for sporogenesis; each cell of the young antheridium contains numerous plastids but the number is reduced to one in the antherozoid mother cell; and in this plant each plastid arose from a pre-existing plastid, there being complete genetic continuity of the plastids throughout the life-cycle. He also suggested that, as he could find no other deeply staining body and no radiations, the structure described as a blepharoplast or centrosome is, in Mosses at any rate, simply the plastid of the antherozoid, the cilia being derived from the ordinary cytoplasm. In a later paper Sapehin (1913) considers the relation between chondriosomes and plastids, and describes the occurrence of chondriosomes in all the mosses investigated (species of *Polytrichum*, *Funaria*, *Bryum*, *Mnium*)—Rudolph's failure to find them in *Mnium* he attributes to the use of an unsuitable fixative; they occurred in almost every cell of the gametophyte and sporophyte but were especially abundant in the protonema, the apical cell of the stem, the germ cells, embryo and spore. However, the plastids occurred side by side with the chondriosomes, and the two structures were apparently quite unrelated.

Finally, Scherrer (1913) has made a thorough investigation of *Anthoceros Husnoti* and *A. punctatus*. As he points out, it would be difficult to find a plant so admirably adapted for the purpose in view as *Anthoceros* with its thin thallus (enabling rapid penetration of fixatives), the single large chloroplast in each cell, the absence of oil-bodies and the almost entire absence of fatty material in the cytoplasm, and the fact that in the slender sporogonium all stages in development of the capsule may be traced in a single section. He found that while every cell of the thallus contains a chloroplast, this is derived by division from a pre-existing chloroplast, as is also the case in the sporogonium; that all the cells of both sporogonium and nearly all those of the gametophyte contain chondriosomes, which are absent however from the apical cell and usually also from its youngest segments; that the chondriosomes, which have the same forms as in higher plants, increase in number with the age of the cell in passing backwards from the apical cell; that the chondriosomes are especially numerous in the thallus cells surrounding the *Nostoc*-cavities and those around the sporogonial haustorium as well as those of the haustorium itself, probably indicating that they play a rôle in nutrition; and that in this plant at any rate there can be no question whatever of any morphological relationship between chondriosomes and chloroplasts.

THE GENERAL QUESTION OF THE ORIGIN OF CHROMATOPHORES IN THE HIGHER PLANTS.

Since the work of Pensa and Lewitsky has opened the question of the origin of plastids, in the higher plants particularly, it may not be out of place here to consider briefly the general position with regard to plastids and their origin in the cell and ultimately in the fertilised oosphere or zygote.

The generalisation of Schimper and Meyer, that chromatophores invariably arise from pre-existent chromatophores and thus persist throughout the plant's life cycle and from generation to generation, has never been seriously called in question for certain Algæ with large single chromatophores; and their further view that in all oogamous plants the chromatophores are carried by the female gamete alone has also obtained support and fairly general acceptance. In *Spirogyra*, for instance, as shown by Chmielevsky (1890), the chromatophore of the male cell disappears at conjugation while that of the female cell divides and give rise to the chromatophores of the new plant. Various writers, prior to Pensa and Lewitsky, have however considered that Schimper and Meyer's generalisation may not apply to the higher plants, having failed to obtain evidence of the existence of plastids in the oosphere or the embryo of flowering plants. Almost simultaneously with the publication of Schimper's and Meyer's papers, Mikosch (1885) and Belzung (1887) stated that they could find no chromatophores in the resting seeds which they investigated. Mikosch examined not only seeds and seedlings but also the young leaves of various plants, and in all cases found that the chromatophores arose directly from the cytoplasm, probably by a process of condensation due to loss of water, the bodies thus formed being at first rod- or spindle-shaped but later assuming the typical discoid form of chloroplasts. Belzung investigated the ripening seeds, mature seeds and seedlings of a large number of plants and in his 1887 paper concluded that growth of starch grains can take place without the intervention of leucoplasts, that chloroplasts are formed directly by differentiation of the general cytoplasm, and that chloroplasts may also be formed at the expense of starch grains which have originated in the cytoplasm. Schimper's criticism of his work led Belzung to make further investigations, the results of which he published in 1891 and which simply verified and extended his former conclusions, for he now stated that the young embryo has no chromatophores, that the starch grains formed in it are laid down in vacuoles of the cytoplasm, that the leucoplasts described by other observers are merely the boundaries of vacuoles in the cytoplasm, that the green colour of the embryo in many plants is due to chlorophyll distributed throughout the cytoplasm of the cell, and that chloroplasts are not formed until germination when the green pigment infiltrates into disintegrating compound starch grains and thus a chloroplast arises. Bredow (1890), Famintzin (1893) and more recently Miller (1911) have however stated that chloroplasts are present in resting seeds, though little appears to have been done in the way of testing the Schimper-Meyer theory that chromatophores are present in the oosphere and that these give rise to the whole of the chromatophores of the plant—a theory, it may be said, for which the authors brought forward very insufficient evidence in the form of convincing data so far as the higher plants are concerned.

In order to decide whether the Schimper-Meyer theory is of general application, it is necessary that the history of the chromatophores should be traced throughout the whole life-cycle, and this has only been done in recent years, in the case of flowering plants, by the upholders of the Pensa-Lewitsky view, and in that of Bryophyta by Sapehin and by Scherrer. The two latter writers, as has been seen, dissent from the chondriosome view of plastid origin, and if their conclusions be accepted it would appear that in Bryophyta as in Algæ the Schimper-Meyer theory holds good, at any rate for the forms which have been fully investigated. As pointed out by Lotsy (1907, p. 27), the correctness or otherwise of the Schimper-Meyer view—according to which chromatophore characters are transmitted only in the female line, the chromatophores of the individual offspring being derived from those of the oosphere—might be tested experimentally if hybrids could be obtained between forms with markedly different chromatophores.

As already mentioned, Schmidt regards the work of Pensa, Lewitsky, Forenbacher and Guillermond as merely confirming the Schimper-Meyer theory by applying methods which have made it possible to detect younger stages in the development of chromatophores than could be observed with previous methods of fixation and staining. Similarly one might regard the work of these later investigators as reconciling with the Schimper-Meyer theory the statements of earlier observers who failed to find chromatophores in the oosphere or the embryo or young tissues, and who concluded that chromatophores arise *de novo* by differentiation of the protoplasm simply because their technique did not enable them to see the earliest stages in the growth of these bodies; though, on the other hand, the upholders of the Pensa-Lewitsky view consider that the minute rod- or spindle-shaped bodies observed by Mikosch in living cells were chondriosomes.

Apart from the three chief views put forward, namely, (1) that the chromatophores of higher plants arise *de novo* by some process of differentiation from the general cytoplasm, (2) that they arise from pre-existing chromatophores traceable throughout the life-cycle, and (3) that they arise by modification of special cytoplasmic structures or chondriosomes homologous with the similarly-named bodies in animal cells, two other theories have been put forward which have received little support. Mereschowski (1910) stands as yet alone with the somewhat remarkable theory that the chromatophores of plants, like the green cells found in various animals, are symbiotic organisms and represent green or blue-green Algæ which originally entered the cell as endophytes and have now become symbionts or helots as in the case of the lichen thallus. Schiller (1909) adopted Goldschmidt's chromidial theory and combined it with that of the existence in plants of two independent nuclei corresponding to the meganucleus and micronucleus of certain Protozoa, regarding the chromatophores as representing a meganucleus (Dotterkern); he could find no trace of plastids in resting embryos of *Triticum* and *Phaseolus* but thought they arose later from the nucleolus which passed out of the nucleus into the cytoplasm and there broke up into grains, these losing their stainability with iron hæmatoxylin as they developed into chromatophores.

CHONDRIOSOMES AND MYELIN FORMS.

As already noted, Lundegard in 1910, just prior to the publication of the papers by Pensa and by Lewitsky which challenged the Schimper-Meyer theory and advocated the new view that chromatophores arise from chondriosomes, published his results which led to the view that the so-called chondriosomes of plants are merely deformed leucoplasts. While preparing this account of recent work on chondriosomes I was much struck by the remarkable outward resemblance between these bodies as described and figured by Meves, Lewitsky, Forenbacher and others, and the "myelin forms" described by Nestler and other writers on the biochemistry of lipoids and made a few simple experiments on lines suggested by the work of these writers. On adding ammonia to oleic acid or to olive oil (or on adding water, or various salt solutions, or albumin solution to lecithin), and watching the result on a slide under the microscope, there are formed, as stated by these writers,[1] peculiar and varied structures—rounded, rod-like (long or short and straight or hooked or spirally coiled), dumbbell-shaped, moniliform, etc.—which present the most striking correspondence in form with all the various types of chondriosomes that have been described and figured. Meanwhile there has appeared a paper by Löwschin (1913), who has gone into this matter in some detail, finding that the myelin forms obtained from lecithin resemble chondriosomes in various respects other than mere form—they can be "fixed" (see below) with chromic acid, osmic acid and formalin, but are destroyed by acetic acid. Myelin forms appear to have been first observed in 1886 by Virchow, who found that when nerve fibres are placed in water the axis cylinder swells and escapes as rounded, ovoid or elongated masses ; later it was found that similar bodies are formed when fatty acids or fats or bodies like lecithin are treated with emulsion-producing substances, and that they are simply emulsion forms. In size they vary considerably according to the mass of the material, the fineness of its division, and the chemical and physical characters of the medium; their form depends on the composition of the bodies, their surface tension and the nature of the medium—for instance, elongated forms are produced when there is streaming in the medium. They show both transverse division and longitudinal splitting like that described for chondriosomes, and various changes are observed as they appear, develop and finally disappear—from homogeneous threads (chondriokonts) are developed granular threads (chondriomites) and these may break up into single granules (mitochondria), while the latter in turn may become aggregated to form chains. They are very sensitive to various reagents, alkalis causing them to break up into granules, as is the case with chondriosomes. As Löwschin admits, these extraordinary resemblances between myelin forms and chondriosomes may be mere analogies of no special importance ; in this connexion one must bear in mind the various types of "amœbæ" obtained in foams and in other ways, Leduc's "artificial cells," Burke's "radiobes," etc.

The analogy between myelin forms and chondriosomes apparently goes further than this, however, for according to Fauré-Fremiet, who regards chondriosomes as consisting of an albuminoid or protoplasmic ground-mass combined (either by ordinary chemical union or by adsorption) with a lipoid substance, the fixatives used in the study of chondriosomes (those based on chromic or osmic acids, etc.) render lipoids, or fatty substances in general, insoluble in fat-solvents such as those employed in cytological technique (xylol, alcohol, etc.), while fatty bodies thus "fixed" are stained in exactly the same way as chondriosomes by the staining methods regarded as specific for the latter. According to the same writer, the chondriosomes of Protozoa and of male animal cells show the reactions of fatty acids, while those of the ovum present the characters of ovolecithin, the fatty body being in each case regarded as associated with an albuminoid substance.

---

[1] For descriptions of these myelin forms, see Molisch, "Mikrochemie der Pflanzen," 1913, pp. 109-111, and the literature cited by him.

The work of Fauré-Fremiet and of Löwschin suggests the possibility that chondriosomes may be simply emulsion forms of myelinogenous substances representing plastic food material. In this connexion mention may be made of experiments recorded by Russo (Arch. f. Zellforsch., Bd. 8, 1912), who found that the number of chondriosomes in rabbit ova increased greatly after the injection of lecithin into the animal. Thulin compared the chondriosomes in the muscle fibres of mature insects in the resting state and after work, and found that in the latter case there was a considerable diminution in the number of these bodies, and similar observations have been made by other workers in the case of secretory cells examined before and after secretion.

CHONDRIOSOMES IN FUNGI.

In one of his 1911 papers Guillermond described the occurrence of chondriosomes in the young asci of *Pustularia vesiculosa*, and in 1913 he gave further details and figures of these and also described chondriosomes in a considerable number of other Fungi (*Penicillium*, *Botrytis*, *Endomyces*, various Autobasidiomycetes, Yeasts, etc.). Meanwhile Janssens, Putte and Helsmortel (1913) had confirmed Guillermond's discovery of chondriosomes in *Pustularia* and had also found them in Yeasts. In one of his 1913 papers Guillermond discusses the function of the chondriome (collective term for the chondriosomes of the cell or the plant) in Fungi. He distinguishes three kinds of reserve-substance products in the asci of *Pustularia*—glycogen, fat globules, and the "metachromatic corpuscles" of earlier writers—and claims to have shown that the last-named bodies arise from chondriosomes in much the same way that plastids arise from the chondriosomes of the higher plants, every transition between chondriokonts and metachromatic bodies having been observed. Hence he ascribes to the chondriosomes the same secretory function as that claimed for these bodies in both plant and animal gland cells. Lewitsky (1913) has confirmed Guillermond's observations, having found chondriosomes in the mycelial hyphæ, conidia and sexual organs of *Albugo Blitii* and *A. candida*; he found that like the chondriosomes of higher plants they were deformed by fixatives containing acetic acid or alcohol but were conserved by fixatives like osmic and chromic acids and formalin, and that they showed the various forms characteristic of chondriosomes in higher plants. As they grew in size they became differentiated into a clear yellow central portion and a deeply staining envelope, the latter representing the substance of the original chondriosome itself. What the yellow substance produced in the chondriosomes may be Lewitsky was unable to determine, but it gave no appreciable darkening with osmic acid and thus seemed quite distinct from the fat globules in the cytoplasm which apparently arise simply by the fusion of originally minute oil drops—Lewitsky could find no trace of elaioplasts or oil-secreting bodies such as have been described for various plant and animal cells.

Conclusion.

In looking back upon the preceding summary—in which it is believed that most of the relevant botanical literature of the subject has been noticed, though doubtless some work on the zoological side has been overlooked—it is fairly obvious that at present there is some difficulty in arriving at any safe generalisations or conclusions regarding the nature of the various bodies to which the term chondriosome has been applied by different writers. It is equally obvious that a sharp distinction must be drawn between chromidial bodies which arise by extrusion of chromatin from the nucleus, assuming that the observations of the actual extrusion of such bodies are correct, and the various other bodies which have been shown to have no such genetic relation to the nucleus. The evidence as to the existence of true chromidia in plants is somewhat scanty and unconvincing, for while it can hardly be doubted that portions of nuclear chromatin may pass into the cytoplasm from nuclei undergoing degeneration, as in the tapetum cells of pollen-sacs, it is doubtful whether these have anything in common with the typical chromidia of certain Protozoa. Goldschmidt's view that chromidia of nuclear origin are of widespread occurrence in animal tissues need not be further discussed here, since we are mainly concerned with vegetable cytology, but it may be noted that even in the Protozoa there is evidence of the existence of chondriosome-like bodies of non-nuclear origin.

When we take into consideration the various statements made regarding the nature and function of the bodies of non-nuclear origin which have been described in plant cells and which have been collectively termed chondriosomes, it must be admitted that at present the literature of the subject raises many questions while it can hardly be said to have definitely solved any. It remains for future work to show whether the chondriosomes of plants (and animals) are actually *sui generis* cell-organs which like the nucleus itself persist from generation to generation—in which case they might well possess the important rôle in heredity assigned to them by Meves; whether they are on the other hand merely artefacts in the sense of being myelin or emulsion forms produced by the action of emulsifying reagents upon fatty or lipoid substances, or (in plants possessing chromatophores) leucoplasts deformed by the action of fixative reagents; whether their function, or one of their functions, in plants is to give rise to chromatophores; and so on.

Whether or not the data already accumulated regarding these bodies be regarded as sufficient for the formation of any definite conclusions on these and various other points, there can be no doubt that the observations and theories here summarised have raised or brought into prominence many interesting problems, besides introducing improved methods of microtechnical investigation and opening up new fields for further work in vegetable cytology and physiology.

LITERATURE.

(The following list is limited to publications on Plant Chondriosomes, and on the Origin of Chromatophores in Plants, starting from the year 1904. Several of the works here listed give citations of the much more extensive zoological literature on Chondriosomes and Chromdia, and of earlier work on Chondriosome-like Bodies in Plants, Origin of Plant Chromatophores, etc.).

Arnoldi, W., et Börnicke, L. "Sur l'appareil chromidial chez quelques plantes gymnospermes et angiospermes." Biol. Arb. til. E. Warming 70 Aars Föds., 1911, pp. 193–201.

Beer, R. "On the Development of the Pollen Grain and Anther of Some Onagraceæ." Beih. z. Bot. Centralbl., Bd. 19, 1905, pp. 286–311.

Bonaventura, C. "Intorno ai mitocondri nelle cellule vegetali." Bull. Soc. Bot. Ital., 1912, pp. 156–165.

Bonnet, J. "L'ergastoplasma chez les végétaux." Anat. Anz., Bd. 39, 1911, pp. 67–91.

Derschau, M. von. "Ueber Analogien pflanzlicher und tierrischer Zellstrukturen." Beih. z. Bot. Centralbl., Bd. 22, Abt. 1, 1907, pp. 167–190.

,, "Beiträge zur pflanzlichen Mitose, Centren, Blepharoplasten." Jahrb. f. wiss. Bot., Bd. 46, 1908, pp. 103–118.

,, "Ueber Kernbrücken und Kernsubstanz in pflanzlichen Zellen." Arch. f. Zellforsch., Br. 7, 1911, pp. 424–446.

Duesberg, J., and Hoven, H. "Observations sur la structure du protoplasme des cellules végétales." Anat. Anz., Bd. 36, 1910, pp. 96–100.

Forenbacher, A. "Die Chondriosomen als Chromatophorenbildner." Ber. d. deutsch. bot. Ges., Bd. 29, 1911, pp. 640–660.

Guillermond, A. "Sur les mitochondries des cellules végétales." Comptes rendus, T. 153, 1911, pp. 183–185.

,, "Sur la formation des chloroleucytes aux dêpens des mitochondries." Ibid., p. 290.

,, "Sur l' origine des leucoplastes et sur les processus cytologique de l'élaboration del'amidon dans le tubercule de pomme de terre." Ibid., pp. 1492–1494.

,, "Sur les leucoplastes de *Phajus grandifolius* et leur identification avec les mitochondries." Ibid., T. 154, 1912, pp. 286–289.

,, "Sur le mode de formation du pigment dans la racine de Carotte." Ibid., pp. 411–414.

,, "Sur les mitochondries des organes sexuels des végétaux." Ibid., pp. 888–891.

,, "Nouvelles remarques sur l'origine des chloroleucites." C. R. Soc. Biol., T. 73, 1912, p. 86.

,, "Sur les différents modes de formation de leucoplastes." Ibid., 1912, p. 110.

,, "Quelques remarques nouvelles sur le mode de formation de l'amidon." Ibid., p. 276.

,, "Sur le mode de formation des chloroleucites dans les bourgeons des plantes adultes." Ibid., p. 459.

,, "Recherches cytologiques sur le mode de formation de l'amidon et sur les plastes des végétaux (leuco-, chloro- et chromoplastes)." Arch. d'anat. microsc., T. 14, 1912, pp. 309–428.

,, "Nouvelles observations sur le chondriome des Champignons." Comptes rendus, T. 156, 1913, pp. 1781–1784.

,, "Sur la formation de l'anthocyane au sein des mitochondries." Ibid., pp. 1917–1919.

,, "Sur le rôle du chondriosome dans l'élaboration des produits de réserve des Champignons." Ibid., T. 157, 1913, pp. 63–65.

,, "Sur les mitochondries des Champignons." C. R. Soc. Biol., T. 74, 1913, pp. 618–621.

Guillermond, A. "Sur l'étude vitale du chondriome de l'épiderme des pétales d'Iris germanica et de son évolution en leuco- et chromoplastes." Ibid., pp. 1280–1283.

Janssens, F. A., Putte, E. van de, et Helmsmortel, J. "Le chondriosome dans les Champignons." La Cellule, T. 28, 1913, pp. 448–452.

Lewitsky, G. "Ueber die Chondriosomen in pflanzlichen Zellen." Ber. d. deutsch. bot. Ges., Bd. 28, 1910, pp. 538–546.

,, "Vergleichende Untersuchungen über die Chondriosomen in lebenden und fixierten Pflanzenzellen." Ibid., Bd. 29, 1911, pp. 685–696.

,, "Die Chloroplastenanlagen in lebenden und fixierten Zellen von *Elodea canadensis*." Ibid., pp. 697–703.

,, "Die Chondriosomen als Sekretbildner bei den Pilzen." Ibid., Bd. 31, 1913, pp. 517–528.

Lotsy, J. P. "Vorträge über botanische Stammesgeschichte. Band I." Jena, 1909.

Löwschin, A. M. "Myelinformen und Chondriosomen." Ber. d. deutsch. bot. Ges., Bd. 31, 1913, pp. 203–209.

Lundegard, H. "Ein Beitrag zur Kritik zweier Vererbungshypothesen." Jahrb. f. wiss. Bot., Bd. 48, 1910, pp. 285–378.

Mereschowski, C. "Natur und Ursprung der Chromatophoren im Pflanzenreiche." Biol. Centralbl., Bd. 30, 1910.

Meves, F. "Ueber das Vorkommen von Mitochondrien bezw. Chondriomiten in Pflanzenzellen." Ber. d. deutsch. bot. Ges., Bd. 22, 1904, pp. 284–286.

Meyer, A. "Bemerkungen zu G. Lewitsky: Ueber die Chondriosomen in pflanzlichen Zellen." Ber. d. deutsch. bot. Ges., Bd. 29, 1911, pp. 158–160.

Miller, E. C. "The Origin of the Chloroplasts in the Cotyledons of *Helianthus annuus*." Bot. Gaz., Vol. 51, 1911, pp. 378–384.

Nieolosi-Roncati, F. "Formazioni mitocondriali negli elementi sessuali maschili dell'*Helleborus foetidus*." Rend. Ac. Sci. Napoli, Ser. 3, T. 16, 1910, pp. 109–119.

,, "Genesi dei cromatofori nelle Fucoidee." Bull. Soc. Bot. Ital., 1912, pp. 144–149.

,, "Contributo alla conoscenza cito-fisiologica delle glandule vegetali." Ibid., 1912, pp. 186–193.

Pensa, A. "Alcuni formazioni endocellulari dei vegetali." Anat. Anz., Bd. 37, 1910, pp. 325–333.

,, "Osservazioni di morfologia e biologia cellulare nei vegetali." Arch. f. zellforsch., Bd. 8, 1912, pp. 612–663.

Rudolph, K. "Das Chondriom der Pflanzenzelle." Sitzber. "Lotus" Prag. Bd. 60, 1912, pp. 197–199.

,, "Chondriosomen und Chromatophoren. Beitrag zur Kritik der Chondriosomentheorien." Ber. d. deutsch. bot. Ges., Bd. 30, 1912, pp. 605–629.

Sapehin, A. A. "Ueber das Verhalten der Plastiden im sporogenen Gewebe." Ber. d. deutsch. bot. Ges., Bd. 29, 1911, pp. 491–496.

,, "Untersuchungen über die Individualität der Plastide." Ibid., Bd. 31, 1913, pp. 14–16.

,, "Ein Beweis der Individualität der Plastiden." Ibid., 1913, pp. 321–324.

Scherrer, A. "Die Chromatophoren und Chondriosomen von *Anthoceros*." Ber. d. deutsch. bot. Ges., Bd. 31, 1913, pp. 493–500.

Schiller, J. "Ueber die Entstehung der Plastiden aus dem Zellkern." Oesterr. bot. Zeitschr., Bd. 59, 1909, pp. 89–91.

Schmidt, E. W. "Pflanzliche Mitochondrien." Progr. rei bot., Bd. 4, 1912, pp. 163–181.

,, "Neuere Arbeiten über pflanzliche Mitochondrien." Zeitschr. f. Bot., Bd. 4, 1912, pp. 707–713.

Smirnow, A. E. von. "Ueber die Mitochondrien und den Golgischen Bildungen analoge Strukturen in einigen Zellen von *Hyacinthus orientalis*." Anat. Hefte, Bd. 32, Abt. 1, 1906, pp. 143–153.

Tischler, G. "Ueber die Entwickelung des Pollens und der Tapetenzellen bei *Ribes*-hybriden." Jahrb. f. wiss. Bot., Bd. 42, 1906, pp. 545–578.

THE
NEW PHYTOLOGIST.

VOL. XIII, NOS. 6 & 7. JUNE & JULY, 1914.
[PUBLISHED JULY 28TH, 1914.]

XEROPHYTIC ADAPTATIONS OF BRYOPHYTES IN RELATION TO HABITAT.

BY W. WATSON, B.SC.

[WITH THREE FIGURES IN THE TEXT.]

(*continued from p. 169*).

(*e*) *Cuspidate Tufts.* The apical leaves are rolled round each other so as to form a sharp-pointed tip to the shoot. Wheldon (25) says that "many tufted mosses growing in open places have long-pointed leaves which in dry weather are closely appressed to the stem, the cuspidate apices of which present themselves as foci for the condensation of dew which drains down the stems, some being retained in the concavity of the leaves." This character is not confined to xerophytes, in fact, the plant (*Hypnum cuspidatum*) in which it is most prominent is usually a plant of marshy places, but by no means always so, as I have found it on dry limestone rocks and walls, probably where surface water occasionally overflowed. This dry ground form scarcely differed from the marsh one except that the colour was darker, the cells narrower, and the cuspidate tips more tightly twisted than usual. Cuspidate tips are also well shown in *H. aduncum* v. *pungens* and in forms of some other *Hypnum* spp.

(*f*) *Leaf Squarrose in the Moist State.* This appears to have little relation to xerophily, since most plants in which it appears are mesophytic or hydrophytic. *Tortula ruralis*, which grows on roofs and walls, has squarrose leaves, but it also has hair-points, spiral twisting, recurved margins to the leaves and papillose cells. Other squarrose-leaved plants with a xerophytic tendency are *T. ruraliformis*, *Barbula recurvifolia*, *Weisia squarrosa*, *Pleurochæte squarrosa*, *Grimmia subsquarrosa*, *Brachythecium reflexum* and *Hypnum Halleri*. On the other hand *Hylocomium squarrosum*, *Hypnum Sommerfeltii*, *Eurynchium prælongum* and its variety

Stokesii, are at most semi-xerophytic, whilst *Dicranella squarrosa*, *Paludella squarrosa*, *Hypnum stellatum*, and *H. riparium* are usually found in wet situations.

The xerophytic squarrose-leaved plants, however, have the peculiarity that the leaves, during drying, change their positions by curling, whereas in the other cases little alteration occurs. The squarrose leaf will certainly absorb water quickly, and in some cases the recurved apices have little chlorophyll, and form the external portions of the shoots (e.g., *H. squarrosum*). Grebe (8) states that the squarrose leaves of acrocarpous mosses have a similar structure to that of the curly mosses, having large, hyaline, extended cells below, and a close-meshed tissue above, but constantly have a broader lamina and a different structure of the midrib.

(*g*) *The Falcate and Secund Leaves* of many Dicranaceæ and Hypnaceæ alter little during different states of humidity, but their importance often seems to be connected with protection from dryness, since one leaf forms a kind of protective hood to that beneath it, and at the same time a number of small water-reservoirs are formed. Falcate leaves are those in which the leaf is sickle-shaped; secundity is said to occur when the upper portion of the leaf is oblique to its insertion on the stem. *Neckera complanata* in a dry state often has the tips of the shoots falcate, and when *N. crispa* grows on dry limestone this is the usual state and is the so-called variety *falcata*. Falcation and secundity are often associated, as in the xerophytic *Dicranum* spp. and in forms of *Dicranella heteromalla*. The falcato-secund character of the leaves is very pronounced in *Hypnum molluscum* (Fig. 3, *13*) when it is growing on dry limestone, as well as in dry-habitat forms of *H. cupressiforme* and *H. uncinatum*, though no definite relation can be established between the degree of falcato-secundity and the nature of the habitat.

The presence of secundity and falcation in many water plants prevents us from regarding it as primarily connected with xerophily, though many of these plants grow in boggy localities, or in places where the water is liable to be dried up, e.g., *Hypnum lycopodioides* in fairly shallow pools of sand-dunes, *H. fluitans* and *H. exannulatum* in moorland pools, *H. riparium* v. *subsecundum* in drier places than where the type grows (23).

Some liverworts also exhibit these characteristics, though in a slighter degree, *e.g.*, some species of *Sphenolobus*, *Herberta*, *Adelanthus* and *Pleurozia*.

(8). CAPILLARY STRUCTURES.

A quick method of obtaining water is necessary when the supply is intermittent or limited, and any capillary apparatus will therefore assist a plant to maintain its local habitat. Many instances of capillary action have been alluded to already under the heads of other protective devices. It must be borne in mind that the presence of capillary apparatus does not show that the bryophyte is a xerophyte, as they are often found in plants growing in moist places, it simply indicates that the plant is capable of continuing its existence under drier conditions than if this method of obtaining water were absent and other conditions were similar.

The following notes on the extremely varied forms of capillary apparatus give some of the chief points of interest in connection with this protective method.

(*a*) *Paraphyllia* (Fig. 3, *24*, *25*). These small supplementary leaves are considered by Goebel to be stem-borne protonemal branches which have developed into cell-surfaces and cell-threads (7), and are also extra assimilatory organs since they contain chlorophyll. They are found chiefly in mesophytes and hydrophytes, though *Thuidium recognitum*, *T. Philiberti* and the paraphyllose species of *Hylocomium* have fairly good claims to be considered semi-xerophytes, as they are often found on dry ground or rock. Other plants having these organs are *Eurynchium prælongum*, *Amblystegium filicinum*, *Hyocomium flagellare*, *Hypnum commutatum*, *H. falcatum*, and other species of *Thuidium*, besides those previously mentioned. In forms or varieties of these plants which grow in wetter places, the paraphyllia are often fewer or absent, as in *Amblystegium filicinum* var. *Vallisclausæ* (=*Cratoneuron Formianum*) and *H. falcatum* v. *virescens*.

Paraphyllia are also present on the calyptra of *Trichocolea tomentella* (14) and *T. paraphyllia* (7).

(*b*) *Tomentum on Stem.* Rhizoids are generally present on the stem in creeping bryophytes, as in most liverworts and pleurocarpous mosses, being sometimes especially abundant, as in *Hypnum commutatum*, *Amblystegium filicinum*, *Lophozia alpestris*, *Gymnomitrium crassifolium* and in the wall form of *Hypnum cuspidatum* previously mentioned. Even in erect-stemmed acrocarpous mosses they are sometimes so abundant as to form a thick network, e.g., *Polytrichum strictum*, *Bryum pseudotriquetrum*, *B. binum*, *B. pallescens*, *Aulacomnium palustre*, *Anoectangium compactum*, *Dicranum scoparium* v. *paludosum*, *D. undulatum*, *D. elongatum*, *Fissidens*

Curnowii, and some species of *Campylopus*, *Philonotis*, *Bartramia*, *Encalypta* and *Swartzia*.

In *Polytrichum* the rhizoids are sometimes aggregated in strands suggestive of the rhizinæ of lichens, and in *Hypnum* they are often produced from the apex or surface of the leaf, e.g., *H. stramineum*, *H. fluitans*, *H. falcatum*.

The presence of rhizoids in the furrows of the gametophore of Marchantiaceæ renders a conducting strand unnecessary. The tubercular rhizoids make possible the maintenance of a more copious supply of water than the smooth ones do, as the size of the resistant air-bubble is more limited (7). The oblique end-walls of rhizoids also aid conduction, owing to the increased contact between the two cells.

In the terrestrial form of *Riccia fluitans* rhizoids are more numerous than in the aquatic form, and Cavers (4) mentions that rhizoids increase in number in the xerophilous and decrease in the hydrophilous forms of *Reboulia*.

(*c*) *Filamentous or Lamellar Outgrowths*, which serve as organs of assimilation or reproduction, also act in a capillary manner. As examples may be mentioned the chlorophyllous plates on the leaves of *Polytrichaceæ*, *Tortula pusilla*, *T. lamellata*, and *Gottschea sciurea* (7), the assimilating filaments of the *Aloina* section of *Tortula* (Fig. 3, *15-17*), the filiform appendages in the axils of the leaves of *Plagiothecium silvaticum* and *P. denticulatum*, the cilia at the base of the leaves or under-leaves in *Œdipodium*, many species of *Lophozia*, and *Lophocolea cuspidata*.

(*d*) *Modified Branches with Small Leaves*, as the filamentous offshoots of *Plagiothecium elegans*, the gemmiform ramuli of *Leucodon sciuroides*, the axillary flagella of *Dicranum flagellare*, the innovations of *Bryum*, and the pendant branches of *Sphagnum intermedium* and some other *Sphagna*. The flagella in *Webera nutans* are not pronounced, but if a wet-ground form is gradually deprived of its water-supply, long, slender, distant- and small-leaved shoots may be induced, especially if the retarding action of light be eliminated.

The flagella of hepatics are similar, and sometimes take root so as to increase the absorptive areas of the plants. They are found in *Bazzania*, *Lepidozia*, *Hygrobiella*, and some species of *Cephalozia*. *Lepidozia reptans* (Fig. 2, *1*) has more flagella than its ally (*L. Pearsoni*) of wetter ground. In damp situations the flagella of *Cephalozia bicuspidata* are more numerous than in aquatic habitats; its relative (*C. Lammersiana*) is a larger plant, has no flagella and is generally found in wetter places.

(*e*) *A Persistent Protonema* enlarges the area from which moisture may be obtained, and as it also increases the bulk of the plant must also assist in the conservation of moisture. When, owing to drought, the protonemal filaments become dried up, the evaporation from the surface of the soil is retarded by its covering of dried-up filaments. The thalloid protonemata of *Sphagnum*, *Tetraphis*, *Œdipodium*, *Andreæa*, *Schistostega* and *Diphyscium* may also act in a capillary manner, but their biological significance is in their assimilatory functions, whilst the discoid protonemata of some Andreæeæ and many liverworts act as water-storers.

(9). VEGETATIVE METHODS OF REPRODUCTION.

These bear some relation to xerophily, as is evident on studying the distribution of brood-bodies, these being found chiefly amongst the plants which prefer dry habitats. During sexual reproduction and the growth of the zygote, greater quantities of food and moisture are required than in the ordinary life of the gametophyte, and the partial elimination of the sporophyte, being concomitant with a reduction in the amount of water required, must have some influence on the habitat of the bryophyte. Gemmæ are produced in a very large number of species of both mosses and liverworts ; filiform ramuli in *Plagiothecium elegans*, *Leucodon sciuroides*, *Fissidens Curnowii*, *Dicranum flagellare*, some species of *Neckera* and *Grimmia*, many species of *Bryum*, *Amblystegium compactum*, *Lejeunea cavifolia* and some species of *Bazzania*, *Aplozia*, *Eucalyx*, *Hygrobiella*, *Eremonotus*, *Radula*, *Herberta*, *Adelanthus*, etc. In some plants proliferating runners or stolons are formed as in some species of *Thuidium*, *Hylocomium*, *Mnium*, *Eurynchium*, *Brachythecium*, *Plagiothecium* and *Hyrcomium*, in others detached portions form a ball and may be carried some distance by the wind, e.g., *Weisia tortilis*, *Porotrichum alopecurum*, *Trichostomum tortuosum*. Deciduous leaves and shoots are formed in *Campylopus*, the protonema is often more or less persistent and almost any part of the plant is able to propagate the species. The fallen leaves of *Campylopus*, *Trichostomum nitidum*, *Barbula sinuosa*, etc., no doubt chiefly aid in retarding evaporation by covering the living plant with dead material.

Dormant buds may also be mentioned here. Drying may take place to such an extent that the outer leaves perish, only the inner leaf-buds protected by the encircling and perishing leaves remain alive and resume activity on the return of moister conditions. In some plants of mobile soil (e.g., *Tortula ruraliformis* and *Trichostomum flavovirens* of sand-dunes), most of the plant is buried in the soil, the apices being thus preserved from desiccation.

B. WATER-STORAGE METHODS.

Many of the methods by which water is quickly absorbed and then stored up by the plant have been briefly alluded to in the previous pages, for the same apparatus often serves a double purpose not only forming small water-reservoirs but also preventing evaporation. Every little contrivance for retaining water is taken advantage of and a device which is of infinitesimal use in a large vascular plant becomes important in these small plants. The following are the most important methods by which water is stored up.

(1). Water-Sacs.

The under-lobes of the leaves of a large number of Hepaticæ are modified to form water-sacs. These are very definite in shape, forming a distinct oval or elliptical bag with a narrow mouth in *Frullania* (Fig. 2, *10*), *Pleurozia*, *Polyotus* (7). In *Colurolejeunea* the water-sac is a pouch-like body, and sometimes has a valve which opens inwards but not outwards.

Water-sacs are also found in some thalloid liverworts. Some of our indigenous hepatics have little pits which retain water, but these can scarcely be dignified by the name of water-sacs; however, some foreign liverworts (e.g., *Metzgeria saccata*, *Dendroceros foliatus*) have outgrowths on the thallus which have a similar hood-like character to those of *Frullania* (7).

Water-sacs may be formed by the two lobes of the leaf being laid against each other, so that a small chamber is formed; the water trickles down the stem, is collected in the lobes, so that none is lost. This is a common method amongst liverworts, and is also shown in the moss *Fissidens* (Fig. 3, *14*). Their best development is shown in the Lejeuneæ—*Cololejeunea*, *Microlejeunea*, *Drepanolejeunea*, *Harpalejeunea*, *Marchesinia*, *Lejeunea cavifolia* (Fig. 2, *2*), *L. patens*, *L. Macvicari*, etc. They are also present in species of *Radula*, *Scapania*, *Diplophyllum*, and *Madotheca*. This apposition of the two lobes is not confined to terrestrial species, but is best defined in them, the aquatic plant often having the lobes very widely divergent as I have found to be the case with *Scapania undulata* when growing in clear springs on Millstone Grit (Fig. 2, *8*, *9*). In *Lejeunea cavifolia*, the variety *planiuscula* of wetter places has the postical lobes almost obsolete.

In *Fissidens* (Fig. 3, *14*) the lower part of the leaf is conduplicate and partially embraces the stem, so that not only is the evaporating surface reduced, but small chambers are formed, thus enabling the plant to absorb the water quickly and afterwards retain it. To compensate for the loss of assimilating surface the nerve has become prolonged and adventitious tissues (superior and inferior laminæ) have been formed on it.

The sheathing leaf is also of service in providing protection against dryness, not only by the decrease of evaporation owing to the sheathing base of the leaf, but chiefly owing to the small reservoirs formed between the stem and the sheathing portion, the latter consisting of colourless, firm and extended cells. The sheathing leaf is shown in *Bartramia ithyphalla*, *Dicranum uncinatum*, *Swartzia inclinata*, and some species of *Dicranella*, but attains its greatest development in *Polytrichum*.

The apex of the shoot forms a cup-like rosette of leaves in some plants (e.g. *Encalypta*). In the damp condition the rosette opens out, takes in dew or rain-drops, but closes up on the return of dryness. The leaf-cups of *Tetraphis* are gemma-bearing rather than water-storing, and many similar rosettes serve for holding antheridia and archegonia.

(2). WATER-STORING CELLS.

(*a*) *Inflated and Hyaline Cells of the Leaf-base* serve as water reservoirs, as well as being of importance in connection with the mechanics of the position-changes in leaves (8). The walls of these cells are thin and often perforated by small pores (especially when their walls are thickened as in *Encalypta*), so that water may be absorbed quickly; they then become swollen out and act as water-storers. Owing to being concealed by the overlapping parts of other leaves, their usual thin-walled nature is of no disadvantage to them during dry weather, as they are screened from the effects of wind and sun. The leaves of these bryophytes are often appressed or curled when dry, becoming more or less patent on being moistened so that they retain any water running down to them. The amount and position of this tissue varies in different plants. In *Polytrichum* it fills up the leaf-base; in *Weisia*, *Trichostomum*, *Rhabdoweisia* and many liverworts a similar position is occupied but not so high up; in *Tortula* and *Encalypta* it lies in the middle portion of the leaf-base, whilst in *Ulota* spp., *Pleurochæte squarrosa*, *Trichostomum flavovirens*, *T. nitidum*, *T. fragile*, *T. inclinatum*, *T. tortuosum*, and *Brachythecium albicans*, the hyaline cells extend up the margin of the leaf.

True auricles, or hyaline-celled distensions of the leaf-base found in species of *Campylopus*, *Dicranodontium*, *Dicranum*, *Dicra-*

nella, *Eurhynchium*, *Brachythecium*, *Plagiothecium*, *Amblystegium*, and *Hypnum* are not confined to xerophytes, though their function may be of a similar nature.

(*b*) *Hyaline Cortical Cells of the Stem* are found in some plants, which are apparently hydrophytic (e.g., *Sphagna* and *Hypnum pellucidum*) and have a similar function.

(3). MUCILAGINOUS CELLS.

Mucilaginous cells absorb a large quantity of water which can then be distributed to the plant according to its needs. They are not abundant except in a few plants, but are generally formed during gametangial development and fertilisation, and are often present as mucilaginous hairs at special places which require to be kept moist, such as the growing point (e.g., *Pellia*), gemmæ-forming bodies (e.g., *Blasia*), etc.

(*a*) *Mucilage cells* are present in the thalli of *Conocephalum* (*Fegatella*), *Lunularia*, *Anthoceros*, *Grimaldia*, etc.

(*b*) *Symbiotic gelatinous Algæ*. *Nostoc* and other Cyanophyceæ is present in special cavities in the Anthocerotales (3) and *Blasia*.

(*c*) *Associated Algæ* are often found in the axils of the leaves, or otherwise associated with them. They usually have gelatinous walls, and mostly belong to Myxophyceæ (Cyanophyceæ). Species of *Nostoc* are the most common but I have found many others—*Glœocapsa*, *Tolypothrix*, *Oscillatoria*, *Scytonema*, *Chroococcus*, *Glœothece*, *Microcoleus*, *Symploca*, *Phormidium*, *Cylindrospermum*, *Ulothrix subtilis*, *Glœocystis*, etc.

(5). HYPOGEAL TUBERS, ETC.

Hypogeal swellings which not only serve as organs for the provision of reserve material, or for the formation of new plants, but also act as water-storers, *e.g.*, the tubers of *Anthoceros*, *Geothallus* (3), *Fossombronia tubifera* (7) and *Petalophyllum*. The hypogeous "rhizomes" of *Stephaniella*, according to Goebel (7) "are the morphological equivalents of the flagella which are found in many Hepatics, and they are able to grow out into leafy branches."

(6). SUCCULENT TISSUE.

This method of storing water, though common amongst the spermophytes is of infrequent occurrence in the bryophytes, and is never very pronounced.

(*a*) *Succulent leaves*. *Œdipodium*, a rare moss inhabiting earthy crevices of high mountain rocks, and the alpine hepatic *Gymnomitrium crassifolium*, of bare moist soil, have somewhat thick leaves, though neither of them can be considered as truly xerophilous. Wall forms of other plants often have thicker leaves than the forms of moister habitats (*Barbula unguiculata*).

(*b*) *Succulent Thallus.* The thallus of the Marchantiales, Anthocerotales and thalloid Jungermanniales is usually thicker when the plants are growing in drier places than their normal habitats. This is noticeable in the form *crassior* of *Aneura pinguis*, especially so in the extreme form growing in patches on some sand-dunes (14), and the same thing is true for the drier ground forms of *Riccia*, *Conocephalum*, (*Fegatella*), *Marchantia*, etc. In *M. polymorpha* there are two extreme forms, the var. *aquatica*, actually growing in the water, and var. *alpestris* occurring on alpine soil; the latter has a thicker thallus than the type whilst the former has a thinner one.

The structure of the thallus in the Marchantiales also has a fairly direct relationship to habitat. Air-chambers containing assimilatory tissue and communicating with the exterior by small pores are present in many of these, but are absent in plants which are constantly found in wet situations (4), e.g., *Dumortiera*, *Marchantia polymorpha* v. *aquatica*, and *Monoclea*. The air-chambers give a supply of air to the plant when covered with water, and during exposure their walls protect the assimilating tissue from undue evaporation. *Targionia* is one of the best examples of a xerophytic member of the Marchantiales combining many of the devices mentioned.

CONCLUSION.

Some of the xerophytic adaptations found in bryophytes also occur in the vascular plants, but many are peculiar to the group. It must be emphasised that many of the plants mentioned as exhibiting "xerophytic" devices are not xerophytes; the devices simply enable the plant to live under less moist conditions than if they were absent.

In conclusion the writer wishes to acknowledge the kind help and valuable criticism given to him by Mr. Tansley and Dr. Cavers during the preparation of this paper.

LIST OF REFERENCES.

1. Bastit, E. "Recherches anatomiques et morphologiques sur la tige et la feuille des Mousses." Rev. Gén. de Bot., 1891.
2. Braithwaite, R. "The British Moss Flora."
3. Campbell, D. H. "The Structure and Development of Mosses and Ferns." London, 1905.
4. Cavers, F. "Contributions to the Biology of the Hepaticæ." Leeds and London, 1904.
5. ,, "The Inter-relationships of the Bryophyta." New Phytol., 1911.
6. Dixon, H. N. "Student's Handbook of British Mosses." 1904.
7. Goebel, K. "Organography of Plants." 1905.
8. Grebe, K. "Beobachtungen über die Schützvorrichtungen xerophiler Laubmoose gegen Trocknis." Hedwigia, 1912.
9. Haberlandt. "Beiträge zur Anatomie und Physiologie der Laubmoose." Jahrb. f. wiss. Bot., 1886.
10. Irmscher, E. "Ueber die Resistenz der Laubmoose gegen Austrocknung und Kälte." Jahr. f. wiss. Bot., 1912.
11. Kerner, A. "Natural History of Plants." 1895.
12. Loeske, L. "Studien zur gleichenden Morphologie und phylogenetischen Systematik der Laubmoose." 1910.
13. Lorch, W. "Der feinere Bau und die Wirkungsweise der Schwellgewebes bei den Polytrichaceen." Flora, 1910.
14. Macvicar, S. M. "Student's Handbook of British Hepatics." 1912.
15. ,, "Distribution of Hepaticæ in Scotland." Transact. Edinburgh Bot. Soc., 1910.
16. Pearson, W. H. "Hepaticæ of the British Isles." 1900.
17. Stapledon, R. G. "Pasture problems; drought resistance." Jour. Agric. Sci., 1912.
18. Tansley, A. G., and Chick, E. "Notes on the Conducting Tissue-System in Bryophyta." Ann. of Bot., 1901.
19. Warnstorf, C. "Sphagnales," in "Das Pflanzenreich," Heft 51, 1911.
20. ,, "Moss Flora der Mark Brandenburg." 1902.
21. ,, "Kryptogamenflora der Mark Brandenburg." 1902.
22. Watson, W. "Distribution of Bryophytes in the Woodlands of Somersetshire." New Phytologist, 1909.
23. ,, "The Mosses of Somerset." Proc. Som. Archæol. and Nat. Hist. Soc., 1913.
24. West, W. & G. S. "Ecology of the Upper Driva Valley and the Dovrefjeld." New Phytol., 1910.
25. Wheldon, J. A. "Social Groups and Adaptive Characters in the Bryophyta." Lancashire Naturalist, 1911.
26. Wheldon, J. A., & Wilson, A. "Flora of West Lancashire." 1907.

PIONEER INVESTIGATORS OF PHOTOSYNTHESIS.[1]

By R. J. Harvey Gibson.

Professor of Botany in the University of Liverpool.

THE problem of the construction of organic material out of inorganic by green plants in the presence of light has occupied the attention of chemists, physicists and biologists for over a century and a half, and although, thanks to their perseverance, we are now acquainted with the chief facts in this chapter of plant physiology, our knowledge is even yet far from being complete. The questions suggested by the summaries given in recent text-books and the diversity of the answers presented force one to the conclusion that the problem, simple as it may at first sight appear, still awaits final solution, and that biologists, as Timiriazeff has wittily expressed it, must rest content, for a little while longer, to contemplate green leaves locked up in glass bottles, like the philosophers of Balnibarbi who with the aid of similar apparatus taught their pupils how to extract sunbeams from green cucumbers. The "Travels into several remote nations of the world"—commonly called "Gulliver's Travels"—were published in 1726, fifty years after Grew and Malpighi first hinted at the mystery that centres round the performances of a green leaf in sunlight, and perhaps the ingenious Dean had read or heard of their researches and may have appropriated some of the ideas they contained.

One difficulty confronts the modern student that the Academicians of Lagado were happily relieved from, *viz.*, access to reliable accounts of the work of previous researchers in this realm of scientific investigation. The task of compiling a summary of all the researches that have been published on photosynthesis is by no means a light one, for the bibliography of the subject includes the titles of over a thousand books and papers and every number of the "Jahresbericht" or the "Centralblatt" keeps adding to the list. Many of these, it is true, are nothing more than trivial notes or "Vorläufige Mitteilungen," criticisms or replies to criticisms.

---

[1] A paper read to the Botanical Club, Imperial College of Science and Technology, November 4th, 1913.

Still, even neglecting such, there is left over a large body of literature that must be consulted by those who would essay serious research on the subject of the synthesis of organic compounds by green plants. It may be said, of course, that Sachs's famous "History of Botany" is available to draw on as a foundation, but one's faith in that much lauded work is far from being confirmed by a study of some of the original treatises on which Sachs bases his story of the development of Vegetable Physiology.

According to Sachs, Malpighi and Hales were the first to establish the two cardinal points in the doctrine of the nutrition of plants, *viz.*, that "the leaves are the organs which elaborate the food, and that a large part of the substance of the plant is derived from the atmosphere." It is somewhat surprising that Sachs should give Malpighi so much credit, after having just said that "he was in doubt whether the air came from the earth through the roots or from the atmosphere through the leaves, for he had never succeeded in finding openings for the entrance of air in the roots or leaves, but he thought it more probable that the air is absorbed by the roots, because they were well supplied with tracheæ and air has besides a tendency to ascend."

Malpighi's book *Anatomes plantarum idea* was, according to Sachs, "laid before the Royal Society, on December 7th, 1671, the same day on which Grew presented his treatise *The Anatomy of plants begun.*" This statement is entirely misleading, as the minutes of the Royal Society shew. Grew's manuscript had been ordered for printing by the Council eight months previously, *viz.*, on May 11th, 1671, and he presented the published work to the Society on December 7th, the date on which the manuscript abstract of the first part of Malpighi's work was laid before it, which, together with the second part was not published until August 20th, 1674. So far as the anatomy of stems and roots is concerned, Grew undoubtedly has priority, but in the preface to the 1682 edition of his work, Grew states that his chapters on leaves, flowers, fruits and seeds, comprising Book IV, "were presented to the said Society in the years 1676 and 1677." Grew thus had access to Malpighi's book of 1674 before he wrote his own chapters on leaves, although he makes no reference to Malpighi in them.

Grew's account of stomata is as follows:—"But as the skins of animals, especially in some parts, are made with certain open pores or orifices, either for the reception, or the elimination of something for the benefit of the body; so likewise the skins of at least many plants are formed with several orifices or passports, either for the better avolation of superfluous sap, or for the admission of air."

On one of his plates Grew figures leaves of the pine and lily shewing what are undoubtedly stomata, although he does not give them that name, so that it must be admitted that Grew, a contemporary of Malpighi, not only was acquainted with the existence of such apertures but had some idea of their functions. It is scarcely fair to Grew's memory, therefore, to say, as Sachs does, that he "brought nothing to light that could assist the further development of the theory of nutrition."

Again, according to Sachs, Malpighi "never succeeded in finding openings for the entrance of air in the roots or the leaves." On the other hand, Malpighi's description of his Plate XX runs as follows:—"Among the vesicles and network of fibres in most leaves are distributed special little air bellows or gaps which pour out either air or moisture. These gaps are especially evident in the leaves of the Oleander; where each area has four to many pores or mouths, the whole surrounded by a margin bearing numerous hairs."

It is difficult to account for Sachs's statement after reading these sentences, unless by assuming that he had never read Malpighi or that he trusted to some third party for his information as to Malpighi's work.

Malpighi's views as to the part played by leaves in plant metabolism are thus summarised by Sachs: "The liquids mingled together in their long passage through the network of fibres are changed in the leaves by the power of the sun's rays and blended with the sap before contained in their cells, and thus a new combination of the constituent parts is effected, transpiration proceeding at the same time." The original, however, reads thus:—"Hence the active leaves seem to have been contrived by nature for the digestion of food which is their chief function, for that part of the nutrient sap which enters the roots from below and which is not diverted into the adjacent transverse branches, at length slowly reaches the leaves by way of their woody veins; this is necessary so that the sap should linger in the adjacent vesicles and so be mingled with the sap already there and be fermented; in this process the warmth of the surrounding atmosphere is of no little assistance, for it helps it the more readily to evaporate that which is of no service. For this purpose nature has provided the leaf with numerous special glands or bellows for the sweating forth and gradual elimination of moisture, so that the sap, being thereby condensed, may the more readily be digested in the leaves."

It would seem therefore that Malpighi regarded leaves primarily as digestive not as manufacturing organs, and that he thought the digestion was a fermentative process; "the power of the sun's rays," as Sachs phrases it, is concerned in that process however only indirectly, *viz.*, by raising the temperature of the surrounding air and so aiding in the evaporation of what was of no service. How Sachs could have read into Malpighi's words a constructive effect of solar energy on the "blended sap" and at the same time denied to him any knowledge of stomata is incomprehensible.

Hales's contributions to Vegetable Physiology are contained in the first volume of his well-known "Statical Essays" and quite recently an interesting summary of his life and an analysis of his work has appeared from the pen of Sir Francis Darwin, published in Oliver's *Makers of British Botany* (1913). Darwin writes, "Hales, of course, knew nothing of stomata," but on page 160 of the 1731 edition of the Essays we read:—"I found little or no air came either from the branches or leaves except what air lay in the furrows and in the innumerable little pores of the leaves which are plainly visible with the microscope." Hales also was quite familiar with Grew's observations on stomata, for he quotes his statements on the subject.

Darwin also says that Hales "does not in any way distinguish between respiration and assimilation," an opinion scarcely supported by the following sentence:—"We may therefore reasonably conclude that one great use of leaves is what has long been suspected by many, *viz.*, to perform in some measure the same office for the support of vegetable life that the lungs of animals do for the support of animal life; plants very probably drawing through their leaves some part of their nourishment from the air." Crude as was the knowledge of animal physiology in the time of Hales it can scarcely be believed that Hales conceived the lungs to be nutritive organs, and the sentence quoted therefore seems rather to indicate that he regarded the leaves as serving both as a respiratory and as a nutritive apparatus.

Up to the middle of the 18th century, however, it cannot be said that even the foundations of the modern theory of photosynthesis had been laid; nor indeed, was that possible till the composition of the air had been determined and until the establishment of the New Chemistry. In 1754 Black discovered "fixed air," rechristened "carbonic acid" by Lavoisier in 1781. In 1774 Priestly discovered "dephlogisticated air," a discovery which he communicated, a few weeks after he had made it, to Lavoisier who in 1782 renamed Priestley's gas "oxygen." With Lavoisier's further identification of a residual "non-vital air," "azote" or nitrogen, and his analysis of water into hydrogen and oxygen, the way was opened for the two physiologists whose names stand out pre-eminent at the close of the 18th and the dawn of the 19th century—Ingenhousz and De Saussure.

In discussing the work of the founders of Plant Physiology, Sachs is curiously contemptuous of the part played by Priestley—a not uncommon failing of this distinguished botanist when criticising the work of English investigators. "The establishment of the fact," says Sachs, "that parts of plants give off oxygen under certain circumstances did little or nothing to forward the theory of their nutrition; and that was all that vegetable physiology owes to Priestley." It is consoling to find that Sachs dates "the revolution which was effected in chemistry between 1770 and 1780" from the "discovery of oxygen gas by Priestley in 1774." The discovery of the gas itself and the part that discovery played in the New Chemistry founded by Lavoisier, not to mention Priestley's observations on the exhalation of oxygen from green parts of plants in sunlight, surely entitle him to a somewhat more appreciative recognition. A comparison of Priestley's writings and Sachs's comments upon them raises the suspicion that the latter either failed to comprehend Priestley's somewhat old-fashioned English or that he contented himself with an inaccurate summary written for him by one of his pupils. Ingenhousz, in the preface to his "Experiments upon Vegetables," expresses a very different opinion of the value of Priestley's work. "The discovery of Dr. Priestley that plants thrive better in foul air than in common and in dephlogisticated air, and that plants have a power of correcting bad air, has thrown a new and important light upon the arrangements of this world. It shews, even to a demonstration . . . . . . that the air, spoiled and rendered noxious to animals by their breathing in it, serves to plants as a kind of nourishment."

Sachs also says:—"After Priestley had ceased his experiments on plants in 1778"—this is a perfectly gratuitous assumption on Sachs's part—"he observed that there was a deposit of matter in the water in some vessels which he had used for them, and that it gave off a very 'pure air'; a number of further observations taught him that this air was given off only under the influence of sunlight; Priestley himself did not suspect that the deposit in question, afterwards known as 'Priestley's matter' and found to consist of Algæ, was a vegetable substance." Hansen ("Geschichte der Assimilation," Arb. bot. Inst. Würzburg, 1884) also, no doubt following Sachs's lead, writes:—" Priestley behauptete, die Substanz des Bodensatzes sei weder vegetablisch, noch animalisch, sondern eine Substanz eigener Art welche er grüne Materie nannte." These views are scarcely substantiated by a perusal of Priestley's "Experiments and Observations on Different Kinds of Air," published in 1790. Book IX of this famous classic is devoted entirely to "observations and experiments relating to vegetation and respiration" and in it he describes how Mr. Walker, of "English Dictionary" fame, told him that while waiting for a boat to convey him to the Continent, he noted a horse-trough at the principal Inn at Harwich, which the Inn-keeper refused to have cleaned out because he had found that its contents remained sweet when the sides and bottom were "covered by a green substance which is known to be of vegetable nature." Section VI of the same Book deals with the "spontaneous emission of dephlogisticated air from water containing a vegetative green matter" and in the body of the section he states that he "never found it [to give off the gas] except in circumstances in which the water had been exposed to light." In Section VII he says he at first supposed the green substance to be a plant but was "unable to discover the form of one. Several of my friends, however, better skilled in Botany than myself, never entertained any doubt of its being a plant; and I had afterwards the fullest conviction that it must be one. Mr. Bewley has lately observed the regular form of it by a microscope. My own eyes having always been weak I have, as much as possible, avoided the use of the microscope." In the following section, Priestley adds, "It will come most properly under the denomination of the Conferva; but this not being within my province I shall not presume to give it any particular appellation." Priestley's modesty is thus translated by Sachs into ignorance: for he not only "suspected" but afterwards "had the fullest conviction" that the green matter which gave off "pure air" in his tanks was a plant but was content, though not a professed botanist, to regard it as a green Alga! After reading these sections in the "Experiments and Observations," it is impossible to avoid the conclusion that Sachs's estimate of Priestley's contributions to Vegetable Physiology is at least misleading if not actually unjust.

Between the date of Hales's "Vegetable Staticks" and that of Priestley's "Experiments on Air," nothing was published worthy of being regarded as a serious contribution to our knowledge of plant nutrition—unless we include Bonnet's treatise "Recherches sur l'usage des feuilles dans les plantes," published in 1757. The central idea of this pretentious work is one that Bonnet adopted from the mathematician Calandrini of Geneva, *viz.*, that the under side of the leaf absorbed the dew that rose from the soil! Bonnet's rank among the founders of plant physiology cannot be more tersely and accurately defined than in Hansen's scathing words:—"Erst wenn eine Geschichte der falschen Propheten in der Wissenschaft geschrieben werden wird, dann wird Bonnet zu Ehren gelangen, denn er wird in erster Reihe mit aufmarschiren."

Ingenhousz's contributions to the subject of gaseous exchange are expounded in his "Experiments on Vegetables discovering their great power of purifying common air in the sunshine and of injuring it in the shade and at night," published in 1779. His discoveries are abstracted in the preface to his volume, but as the statement is diffuse and couched in old-fashioned terminology it may be convenient to condense and translate it into rather more modern phraseology. "I observed that plants were able to purify bad air in a few hours if subjected to sunlight; that they could transform air absorbed from the exterior into oxygen; that this oxygen is exhaled into the atmosphere thus rendering it more fit for animal life; that the exhalation of oxygen by plants begins after sunrise, is the more active the brighter the day and the more the plants are exposed to solar radiation, and the less active the more they are shaded by buildings or by other plants, when, so far from purifying the air, they contaminate it as animals do; that they cease to exhale oxygen as darkness comes on; that only leaves and petioles carry out this function; that the exhalation of oxygen in sunlight is independent of the poisonous or other quality of the plant; that the oxygen is given off chiefly by the under surfaces of leaves and that the mature leaves, cæteris paribus, give off more oxygen than young leaves; that some plants, especially aquatics, give off more oxygen than others; that, on the other hand, all plants in darkness render the air impure, especially such parts as flowers, fruits and roots, no matter how economically useful they may be; that the sun alone has no power to purify air—it may, indeed, even tend to render it less pure—unless when acting in conjunction with green plants, and finally, that the degree of purity of the air given off by green plants depends on many factors such as the intensity of the light falling on them, the extent of exposure of the leaves to sunlight and so on."

Not a bad record of results, one must admit, when it is remembered that they were all deduced in the year 1778, from something like 500 experiments performed with the crudest of apparatus in three months (June to September) in a villa garden near London in such intervals of leisure as were afforded to a court physician in the reign of George III.

Sachs asserts that Ingenhousz "not only discovered the assimilation of carbon and the true respiration of plants but also kept the conditions and the meaning of the two phenomena distinct from one another." I can find no evidence in the "Experiments on Vegetables" that Ingenhousz had any idea that the "foul air" or the "common air" absorbed by plants contributed anything to their sustenance beyond his quotation from Priestley, *viz.*, "that the air, spoiled and rendered noxious to animals by their breathing in it, serves to plants as a kind of nourishment"—Priestley's own words are "The pabulum which plants derive even from common air." Not till long afterwards, in 1796, when he published his "Essay on the Nutrition of Plants and the Fruitfulness of the earth," was Ingenhousz able to interpret the gaseous interchanges correctly, as he himself admits. He confesses that since the new system of chemistry was not in existence when he wrote his "Experiments on Vegetables," he was not in a position to formulate a suitable theory to explain the facts. Now that he knew that "fixed air" or carbon dioxide was a compound of carbon and oxygen, he found no difficulty in putting forward a comprehensive theory of plant nutrition, so far at least as the plant's relation to air was concerned. He held that green shoots gave off oxygen in sunlight and carbon dioxide in darkness, and that non-green parts gave off carbon dioxide both in the light and in the dark, but he thought that the carbon dioxide was the source both of the carbon retained by day and the oxygen retained at night. From the carbon and oxygen so acquired the plants manufactured their acids, oils, mucilage, etc., and these they combine with atmospheric nitrogen in the organs of their bodies.

In the "Essay" also Ingenhousz says that plants incessantly give out impure air, an indication that at the date of its publication he had grasped the fact of the concomitant existence of the two processes of photosynthesis and respiration. Indeed, he published a paper on the subject in Vienna in 1786, although his statements still exhibit some confusion of thought. As Hansen puts it—"Die Assimilation ist entdeckt, sogar Assimilation und Athmung unterscheiden, wenn auch der letztere Vorgang noch nicht begrifflich und von der Assimilation getrennt."

The years 1770-1790 were fateful years in the history of Chemistry and undoubtedly the genius of that period was Lavoisier. As Liebig says of him, "All the facts established by him were the necessary consequences of the labours of those who preceded him. His merit, his immortal glory consists in this, that he inspired into the body of the science a new spirit." Not the least of his services to science was his refutation of the Phlogiston Theory, based on exact quantitative analysis, and his skilful employment of the balance in experimentation. The extent of Lavoisier's influence, so far as vegetable physiology is concerned, may be readily appreciated by a comparison of the works of Ingenhousz with those of De Saussure.

Another name is prominently put forward by historians as contributing largely to the solution of the problem of photosynthesis, *viz.*, that of Senebier. Senebier's claims to distinction in this branch of physiological enquiry rest chiefly on three publications which, for brevity's sake, may be termed the "Memoires," the "Researches" and the "Experiments." The last-named appeared in 1788 and contains the essential points relative to photosynthesis published in 1800, in what Sachs terms his "tediously prolix work in five volumes the Physiologie Végétale." The first part of the "Experiments" is devoted to a long controversial attack on Ingenhousz, followed by a discussion of what happens to leaves exposed under water in darkness, whether they vitiate the air in darkness when exposed freely or only when enclosed in glass vessels, the effect of heat and moisture on air and of plants in general on phlogisticated, dephlogisticated and inflammable air, etc. Considerably more than half the volume is given up to decidedly "prolix" statements of his views on such subjects and endless experiments in support of them, but it must be confessed that these statements compare unfavourably with the terse and clear sentences of Ingenhousz. The second part deals with the estimation of the amount of air given off by leaves in water charged with different proportions of carbon dioxide, while the third part summarises the results obtained in the preceding chapters.

A perusal of Senebier's works forces one to the conclusion that, though a good observer and a laborious experimenter, he is far from being a clear thinker. His style is frothy and turgid, and he repeats himself again and again, and in this respect offers a marked contrast to Ingenhousz. The latter sets before himself a definite problem and contrives an experiment to prove his point. Senebier, on the other hand, piles experiment on experiment, but leaves his reader to draw the conclusion, for there is little or nothing of a general thesis running through the work to string the experiments together. He repeated Ingenhousz's work on the relation of sunlight to the exhalation of gas from green parts and held that the leaves were the responsible agents for this phenomenon, while non-green parts gave off CO_2 only. He shewed that it was light and not heat that induced the exhalation of oxygen and that this took place only in presence of CO_2. It is generally said that Senebier discovered that the oxygen resulted from the decomposition of CO_2 but I have been unable to discover any evidence to support this view. On the contrary, he says that the plant takes the phlogiston out of the CO_2 and gives off oxygen as an excrement. He thinks that CO_2 is thus changed into oxygen and that the acid character of the CO_2 acts as a stimulant on the leaves to bring about this change. He attempted indeed to induce the exhalation of oxygen by substituting hydrochloric, sulphuric and nitric acid for carbonic acid, but naturally without the desired result. He also believed that the CO_2 entered by the root. Holding such views as these it is scarcely to be expected that Senebier could have had any conception that CO_2 was decomposed into carbon and oxygen when leaves were exposed to sunlight. It is true, he claimed in his "Physiologie Végétale," published in 1800, that he had an idea of the decomposition of CO_2 in 1788, but Ingenhousz had also a suspicion of the same phenomenon in 1779, and at the date of the publication of the general treatise in which he made this claim, Ingenhousz's "Nutrition of Plants" had been before the scientific public for four years, and in it the thesis is clearly enunciated, *viz.*, that carbon dioxide is decomposed in sunlight, that the carbon is retained by the plant and that the oxygen is exhaled. Hansen's estimate of Senebier seems most nearly to approach the truth :—"Demnach kann Senebier weder

als Entdecker noch als Mitentdecker der Assimilation bezeichnet werden. Einiger Verdienst liegt in seinen Experimenten, namentlich in denen ueber die Wirkung der Sonnenlichtes auf den Gaswechsel . . . . . . er sammelt aber er baut nicht auf."

The publication of the "Chemical Researches on Vegetation" by De Saussure in 1804, marks an epoch in the history of plant nutrition. At last the phlogiston theory disappears from chemistry and we meet for the first time with a chemical terminology and chemical methods which may be regarded as, comparatively speaking, modern.

A glance at the headings of the sections of De Saussure's chapters, together with a study of the succinct resumés which he offers at the end of each, enables the reader to form a very clear conception of the general theory of plant nutrition held by the author, and hence it is all the more remarkable that Sachs should characterise the book as "dry and unattractive" and deficient in offering no "deductive exposition [of his doctrines] of a more didactic character." Hansen's estimate of De Saussure's work is much more just: "Das waren die Leistungen eines echten Forschers, der nicht tastete, nicht versuchte, sondern der mit System der Wissenschaft im Kopfe an eine Frage heranging und mit sicherer Hand die Methode handhabte, dieselbe zu lösen."

Investigators before De Saussure's day had attempted little more than a demonstration of the conditions under which carbon dioxide was decomposed and oxygen given off; De Saussure tackled the problem by quantitative methods and so gave clearness and precision to what was previously vague and sketchy.

That the presence of gaseous CO_2 was an essential condition of plant growth was De Saussure's starting point. He recognised that plants could be grown under bell-jars in a CO_2-free atmosphere, but he explained this by saying that they utilised the CO_2 they themselves formed in respiration, for if the CO_2 so formed was removed by KOH or other absorbent as fast as it was formed, then the plant succumbed.

In the second chapter of his book De Saussure discusses the effect of carbonic acid gas on vegetation, and proposes to "ascertain whether this gas is useful to plants when it is derived from the surrounding air." A paper by T. Percival, of Manchester, published, so far as I can discover about 1785, apparently suggested to De Saussure an important line of research. Percival had observed that a plant of mint exposed to a current of air containing an excess of carbonic acid gas over the normal, grew better than a similar plant grown in "pure air," and De Saussure at once set himself the task of determining "the dose of carbonic acid gas which, mixed with air, most favours vegetation." He gives details of his experiments into which it is unnecessary to go; his results, however, are of great interest, for he found that when the air used in his bell-jar consisted of one-twelfth CO_2 (8·3%) and when the plants were exposed to the direct rays of the sun—tempered when the light was too intense—the plants were always healthier than when grown in ordinary air, while that in the shade the slightest dose of carbonic acid gas over the normal added to ordinary air was at once injurious." Seventy and eighty years later, Godlewski and Kreussler carried out a series of experiments on the same subject and arrived at precisely the same results.

De Saussure acknowledges that Priestley "was the first to recognise that leaves were able to purify air vitiated by combustion and respiration," but admits that "he did not explain the cause of this phenomenon." Senebier, on the other hand, is credited with the discovery of the fact that "leaves decompose carbonic acid gas, appropriating its carbon and giving off its oxygen," although it would seem that Ingenhousz has an equal if not a prior claim to the credit of this discovery. De Saussure deals with this—the fundamental photosynthetic problem—in considerable detail, using as his materials plants of *Vinca*, *Mentha*, *Lythrum*, *Pinus* and *Cactus*. One of his conclusions is that "plants in decomposing carbonic acid gas, assimilate a part of the oxygen contained in it." He is more successful with his attempts to prove that "plants fed on pure water and growing freely in air, obtain their carbon from the small amount of carbonic acid gas normally present in the atmosphere."

After a lengthy discussion of the gaseous exchanges exhibited by succulent plants like *Opuntia* and by different foliar types, by roots, woody stems, flowers and fruits, he summarises his results in the following words, "Green plants growing freely in air and exposed to the successive influence of light and darkness, alternately inspire and expire oxygen mixed with carbonic acid gas. Green plants do not immediately assimilate the oxygen they take in; on inspiration it is changed into carbonic acid gas. This is decomposed on expiration and it is only through this (partial) decomposition that they can assimilate the oxygen which is in the air. Speaking generally, non-green parts do not exhibit these successive inspirations and expirations, they neither directly nor indirectly assimilate the oxygen of the air. On the contrary, they change it into carbonic acid gas which may be found in small quantities stored or dissolved in the succulent tissues just as it would be in pure water; otherwise they do not alter it. The carbonic acid which the non-green parts form with the surrounding oxygen traverses the plant, ultimately to be decomposed in the leaves. Leaves of marshy plants, succulents and evergreens grown under otherwise similar conditions use less oxygen than do the leaves of other plants."

In his sixth chapter, section 3, he expresses surprise that in no case could plants decompose carbon monoxide. That plants could utilise this gas has been asserted and denied again and again, *e.g.*, by Stutzer, Just and others. Even as late as 1903, Bottomley and Jackson brought forward fresh evidence of the nutritive value of carbon monoxide, given certain conditions.

The seventh chapter of his book deals with the decomposition and fixation of water by plants, which De Saussure says takes place coincidently with the fixation of carbon :—"Plants appropriate the elements hydrogen and oxygen from water, and in doing so cause it to lose its liquid state, but this assimilation is not very pronounced unless carbon be appropriated at the same time. Water fixed or incorporated by plants can apparently only lose its oxygen in the form of gas after the death of the plant or of one of its parts. As soon as plants which have assimilated the oxygen and hydrogen of water begin to ferment without contact with free oxygen, they then form carbonic acid exclusively from their own tissues. The oxygen of the combined water can then unite with carbon to form carbonic acid gas, and the plants or growing organs in dissociating oxygen from this carbonic acid eliminate indirectly an element originally belonging to the water. Thus by the combined action of vegetation and fermentation operating without contact with air, water can give off its chief element in the form of oxygen. In no case, however, do plants directly decompose water in assimilating hydrogen and in eliminating oxygen as a gas. They never exhale oxygen save as a consequence of the direct decomposition of carbonic acid. Thin-leaved plants growing in pure water in an atmosphere of oxygen and nitrogen—and subjected to the successive influence of light and darkness do not exhale oxygen and give no external indication of the direct decomposition of water. It is impossible to attribute to the direct decomposition of water the oxygen which they emit into an atmosphere of nitrogen, or under water, because whenever oxygen is lacking from their environment they manufacture carbonic acid entirely from their own substance. Some succulents growing in ordinary air without carbonic acid emit a quantity of oxygen, which exceeds several times the volume of the plant. But the gas, which may originally have come from the water, is found, on ultimate analysis, to have proceeded only from the decomposition of carbonic acid gas which the plants form in sunlight from their own tissues. This is proved by the fact that if an absorber of carbonic acid be placed near such plants, oxygen is no longer added to the surrounding air either by day or night. Although their growth may be vigorous, the plants give no indication of direct decomposition of water. The special peculiarity which succulents have of forming carbonic acid from their own substance is due, in part, to the feeble porosity of their epidermis and in part to the slight contact of their internal tissues with the oxygen of the air. There can be no doubt that the major part of the hydrogen, which annuals acquire whilst growing freely in air and in distilled water is derived from the water which they combine. Similarly, in the case of oxygen, for we may conclude both from the amount of carbonic acid the plants can decompose in a given time, and from the slight alteration which they effect on ordinary air, that the amount of oxygen which they imbibe from ordinary air is not sufficient to account for the amount they acquire during the short period of their development. We must not forget that in the decomposition of most dried plants water is the most abundant product formed and that oxygen is the chief constituent of it."

The chief merit of De Saussure's work lies in the rigid scientific methods he employed in his researches, the logical manner in which he marshalled his facts and the careful deductions he draws from them. Doubtless his mental attitude owes much to his intimate association with his father, the distinguished physicist and alpine climber, and perhaps even more to his thorough study of the writings of Lavoisier. By many, De Saussure is spoken of as the last of the little band of investigators in plant physiology who flourished at the end of the 18th and the very early years of the 19th century. Perhaps it would be more correct to speak of him as the forerunner of the new school of chemical biologists represented more than a generation later by Boussingault and Liebig.

If Priestley and Hales were the first to hazard crude suggestions of an interesting plot and if Ingenhousz has the merit of blocking out, though in the rough, the principal acts in the drama, then De Saussure, trained in the school of Lavoisier, may be regarded as the skilled playwright who gave to the various scenes the polish his predecessors, from the very nature of things, could not accord to them, and who arranged them in the sequence necessary to weave them into a logical and convincing story. More than forty years had to elapse befose Daubeny and Draper re-opened De Saussure's Book to outline a new chapter on the kind of light that was concerned in the decomposition of carbon dioxide, a chapter completed in quite recent years by Timiriazeff, Reinke and Engelmann. Another chapter on the first synthetic products was sketched out by Sachs in the early sixties, elaborated by Von Baeyer and later still by Bokorny, Curtius, Pollacci and Loeb, and yet another on the nature of the pigment so closely associated with the photosynthetic phenomena, started by Frémy and Kraus, added to by Schunck and Marchlewski and, at the present moment, by Willstätter and his pupils.

The story is by no means complete even yet, for recent researches by Moore, Stoklasa, Zdobnicky and others, would appear to hint at colloidal iron and ultra-violet light as factors in the process and as taking a great and hitherto unsuspected part in the phenomena, at first sight apparently so exasperatingly simple, yet on further investigation, so complex and elusive as those that take place in a green leaf when exposed to sunlight. Amid the bewildering multiplicity of new facts being brought to light from day to day, and the diversity of explanations offered of the intricate processes summed up under the term "photosynthesis," it is essential to bear in mind how much is owing to the great pioneers who, after all, laid so truly and well the foundations of the temple Modern Botany is now striving to complete.

MORPHOLOGICAL AND BIOLOGICAL NOTES ON NEW AND LITTLE KNOWN WEST-HIMALAYAN LIVERWORTS. I.

BY SHIV RAM KASHYAP, B.A., M.Sc.,
Professor of Botany, Government College, Lahore.

[WITH FOUR FIGURES IN THE TEXT.]

INTRODUCTION.

THE liverworts here described were collected by the writer during the months of August, 1912, and July, August and September, 1913, at Mussoorie.[1] A few visits were paid to the place at other times in order to get an idea of the vegetation throughout the year. Mussoorie is a hill station in the north-western Himalayas, its exact position being 78° 71′ E., 30° 26′ W. Its height above sea-level is about 6,000 feet.

A few words about the climate of the district will not be out of place, as the various adaptations in the plants described will be better understood in the light of the climatic conditions. The most important fact in connection with the climate is that there is a short rainy season, roughly from June to August, while the rest of the year is comparatively dry. The following table shows the rainfall and the number of rainy days for the last five years. I am indebted to Col. C. Milne, Civil Surgeon of Mussoorie, for allowing me the use of the figures which were obtained at the Civil Dispensary.

RAINFALL.

	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Total of Year.	Total of June to Sept.
1909	2·33	3·18	·03	3·11	·68	17·65	32·75	37·45	5·65	·03	·00	2·39	105·35	93·50
1910	1·45	1·10	·00	·88	2·21	9·89	41·00	31·76	9·68	5·80	·27	·32	104·36	92·33
1911	9·94	·55	11·11	·82	·70	4·84	5·14	17·23	8·30	1·70	6·50	·00	66·83	35·51
1912	2·48	1·16	1·98	2·60	1·86	6·78	29·20	43·40	14·59	·00	2·40	1·08	107·53	93·97
1913	·20	6·82	3·22	·09	3·90	25·12	30·70	16·92	—	—	—	—	—	—

---

[1] Many of these species along with some others not mentioned here have been recently found by the writer in another part of the western Himalayas, *i.e.*, the Chamba state.

RAINY DAYS.

	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.
1909	7	9	1	12	2	22	23	26	7	1	0	5
1910	4	5	0	4	6	19	30	28	19	3	2	1
1911	13	2	13	4	2	16	13	16	17	2	3	0
1912	3	4	2	4	4	11	26	30	11	0	1	2
1913	1	9	4	3	10	16	23	19	—	—	—	—

It will be seen from the above that the plants have to pass through a dry period representing the greater part of the year. In addition to the small amount of precipitation, insolation is very strong and evaporation very great, as in all mountain districts. In September, for instance, at the end of the rainy season, a fortnight of uninterrupted sunshine is sufficient to kill a large number of herbs growing as epiphytes or in exposed places.

Connected with the long dry period, we find that many herbaceous plants have developed organs of perennation in the form of tubers, bulbs, rhizomes, etc. As examples may be cited many orchids, aroids, crassulaceous and many other flowering plants, epiphytic ferns, also two species of *Selaginella*[1] and *Gymnogramme leptophylla* with its tuberous prothallus. The liverworts possessing such perennating organs are mentioned below and it will be seen that their number is pretty large. During the rainy season four or five inches of rain in twenty-four hours is not unusual and occasionally the rainfall may reach eight to ten inches. The force of the water on the slopes is naturally very strong and the plants have to be firmly fixed in order to escape being washed away.

The thallose liverworts, including the Anacrogynous Jungermanniales, will be taken first. The latter series, although possessing some foliose forms, is here included in the thallose group as all these plants taken together form essentially one ecological class. Most of the plants described below can be found, with a little careful search, within half a furlong on many more or less exposed eastern slopes. This does not, however, apply to the species of the genera *Cyathodium* and *Cryptomitrium* which are adapted to light of a very low intensity, the hygrophilous genus *Dumortiera*, the genera *Aneura* and *Metzgeria*, and a species of *Marchantia*. The last three are found at a level of about 5,000 feet, *Metzgeria* being an epiphyte.

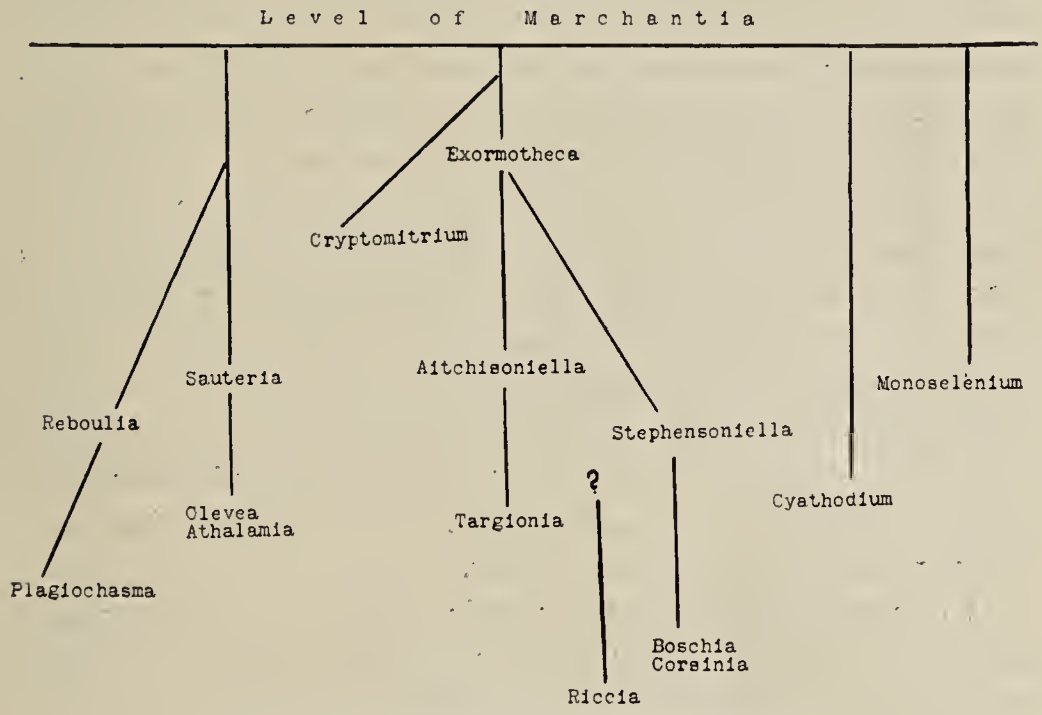
---

[1] *S. chryrorhizos* with underground tubers, and *S. chrysocaulos* with resting buds. My thanks are due to Professor Seward who had these species identified for me.

The following is a list of the thallose forms met with at Mussoorie at a level of 6,000 feet (with the exception of the three species mentioned above). The position of the new genera and species is briefly indicated, as full descriptions are given later. The methods by which these plants pass through the dry period are indicated by letters: A indicates the ability of the plant to revive as a whole after desiccation; B indicates that the apical part only survives, but is not much modified; C that the apex is modified to form a definite tuber; D that ventral or lateral shoots are modified to form tubers. The rest are hygrophilous or annuals. It must be also mentioned that reproduction by spores plays a very unimportant part in this region.

(1) *Riccia discolor* (B). (2) *Targionia hypophylla* (A). (3) *Cyathodium tuberosum*, sp. nov. (C). Male receptacle of composite type. (4) *Aitchisoniella himalayensis*, gen. et sp. nov. (B). Near *Targionia* but female shoot reduced to receptacle. (5) *Athalamia pinguis* Falc. (Trans. Linn. Soc., vol. 20, 1851) (B). Near *Clevea*. (6) *Gollaniella pusilla* St. (Hedwigia, vol. 44, 1905) (B). (7) *Plagiochasma appendiculatum* (A). (8) *P. articulatum*, sp. nov. (A). Receptacles terminal, growth continued by an adventitious shoot. (9) *Reboulia hemispherica* (A). (10, 11, 12) *Fimbriaria*, three species (B). (13) *Grimaldia californica* (A). (14) *Exormotheca tuberifera*, sp. nov. (D). Ventral shoots form tubers. (15) *Stephensoniella brevipedunculata*, gen. et sp. nov. (C). Near *Exormotheca* but growth continued by an adventitious apical shoot after formation of female receptacle. (16) *Cryptomitrium himalayensis*, sp. nov. (C). (17) *Dumortiera hirsuta*, hygrophilous. (18, 19) *Marchantia*, two species, in shady moist places. (20) *Aneura pinguis*, in shady moist places. (21) *Metzgeria hirsuta*, sp. nov. (A). (22) *Pellia calycina*, in moist places. (23) *Fossombronia himalayensis*, sp. nov. (C). (24) *Sewardiella tuberosa*, gen. and sp. nov. (C). Very near *Fossombronia* but thallose. (25) *Notothylas* sp. Annual. (26) *Anthoceros himalayensis*, sp. nov. (D). Ventral and lateral shoots form long-stalked tubers. (27) *Anthoceros erectus*, sp. nov. Annual, with large mucilage cavities. (28) *Massalongoa tenera*, described by Stephani (Hedwigia, Bd. 44, 1905), but not found by the writer.

The general conclusions arrived at by the writer with regard to the evolution of the Marchantiales in the light of the new species may be set forth in a few lines. The detailed discussion will be taken up in connection with individual species. The view expressed by Goebel after his study of *Monoselenium tenerum* (Flora, Bd. 101, 1910) that simpler forms of the Marchantiales are reduced has been strongly confirmed in a general way. It has been possible to work out the relationships in some cases in detail. The following scheme indicates the probable evolution of the Marchantiales by reduction as judged particularly by the position and structure of the carpocephalum and sporophyte.



Suggested Phylogeny of Marchantiales (see Text).

CYATHODIUM, TARGIONIA, AND *AITCHISONIELLA.*

The genera *Cyathodium* and *Targionia* have been placed together by most authors—as Schiffner,[1] Campbell,[2] Lang,[3] Lotsy,[4] Goebel[5] and Cavers[6]—on account of the similarity of the male and female receptacles. Deutsch,[7] however, has recently called attention to the great difference between the two genera, but he has ignored Lang's important contribution to the morphology of *Cyathodium* and has not added any new fact in connection with that genus. The study of *Cyathodium tuberosum* shows that the distance between the two genera is greater than has been supposed up to this time.

[1] Engler and Prantl. "Natürliche Pflanzenfamilien."

[2] "Mosses and Ferns," 1905.

[3] "The morphology of *Cyathodium*." Annals of Botany, 1905.

[4] "Vorträge über Botanische Stammesgeschichte," Band 2, 1909.

[5] "Archegoniatenstudien, XIII. *Monoselenium tenerum*." Flora, Bd. 101, 1910.

[6] "Inter-relationships of the Bryophyta." NEW PHYTOLOGIST, 1910, 1911; New Phytologist Reprint No. 4.

[7] "A study of *Targionia hypophylla*." Bot. Gazette, vol. 53, 1912.

CYATHODIUM TUBEROSUM KASHYAP.

In shape and structure the thallus is like that of *C. cavernarum* as described by Lang. The species under consideration, however, is diœcious and forms tubers. Thus the plants are met with in three forms—sterile, male, and female. The sterile plants are once or twice dichotomously divided and the lobes are linear or linear-oblong. The appearance of the male plants is variable, the lobes being linear or oblong obcordate. The female plants may be linear or linear-oblong, but more often they are fan-shaped with many growing points on the anterior margin due to rapid dichotomy. The narrow plants are usually less than 2 mm. broad, while the large female plants may be as much as 1 cm. long and 2 cm. broad in favourable localities. The plants are usually found in dark and moist places forming dense masses of overlapping individuals. In some cases the only other plant inhabitant of the cave was *Cryptomitrium himalayensis* Kashyap, and under these circumstances both these species have a yellowish phosphorescence. *Cyathodium tuberosum* may, however, occur in only slightly shady places along with *Riccia*, *Targionia*, *Plagiochasma*, *Anthoceros* and other more or less xerophilous forms and even in almost exposed situations, where it develops a deep green colour.

In some sterile and smaller male plants no pores are ever formed. In a large number of them, however, pores are present but on the *ventral* surface. In the larger female plants pores are present on the dorsal surface. Pores on both surfaces were not met with in any plant. The dorsal pores (Fig. 1, *a*) are scattered on the dorsal surface, one being found in one but not in every areole; they are circular just behind the anterior margin but become elongated and elliptic further back. Each pore is surrounded by two or three series of four or five cells each; these cells are narrow and hyaline and peculiar in that the outer walls of the innermost cells are also concave outwards like the inner walls. The transition to the ordinary cells of the thallus is gradual. The ventral pores are much simpler and much larger and elongated in the direction of the longitudinal axis of the thallus (Fig. 1, *b*). They are bounded by ordinary cells of the thallus. All the cells of both the upper and lower layers of the thallus contain chloroplasts but they are more numerous on the dorsal side.

There are two rows of scales on the ventral surface. They may be simple cell rows or small plates (Fig. 1, *c*, *d*). Usually there are no mucilage cells but occasionally a small cell differing from the rest is met with at or near the apex. All cells of the scales contain chloroplasts, as is the case with the scales of *Monoselenium*[1] and the young scales of *Aitchisoniella.*

Both the thick-walled narrow and thin-walled wide rhizoids are present, but the former do not possess the pegs and are much more numerous than the latter. There is no distinct midrib in the thallus.

The ventral pores, apart from their absence in other Marchantiales, are interesting in another respect also. Filaments of *Oscillatoria* and small colonies of *Nostoc* which grow near the plants often find their way into the thallus-chambers through them. In one case even small eggs of some animal were found inside the chambers. This connection between *Cyathodium* and the blue-green algæ mentioned above seems to be quite accidental, but it suggests the method by which a permanent connection may have been established between *Anthoceros* and *Nostoc.*[2]

The ventral pores seem to have been produced in order not to reduce the area of the upper surface available for the absorption of the small amount of available light and at the same time to provide for adequate gaseous exchange.

The apical parts of the sterile plants and the sterile branches of male plants become transformed into tubers about the end of the rainy season, *i.e.*, about the end of August. Short pointed thick-walled hairs begin to appear on the margins and the ventral and dorsal surface of the thallus, a short distance behind the apex. The thallus itself becomes very much denser than it was before near the apex. On the anterior margin there is one growing point which in many cases forks into two before tuber formation. The air chambers are small and numerous and divided by horizontal septa so that there is more than one layer of them (Fig. 1, *e*). There are no pores. The mature tuber (Fig. 1, *f*) is about 1 mm. long and a little broader, firmly fixed to the substratum and covered dorsally and laterally by numerous forwardly directed spike-like hairs, and ventrally by similar hairs and rhizoids. These hairs are obviously modified rhizoids. On the ventral surface there are a few scales. The cells of the tuber contain numerous chloroplasts and some starch. There are one or two growing points on the anterior margin. The margins of the tuber are directed obliquely upwards, so that there is a groove in the mid-dorsal line.

[1] Goebel, loc. cit.

[2] Cavers (Ann. Bot., vol. 18, 1904, p. 91) describes the occurrence of *Nostoc* chains in the ventral tissue of *Fegatella* and several other Marchantiales. It would be interesting to know whether these forms also possess ventral pores.

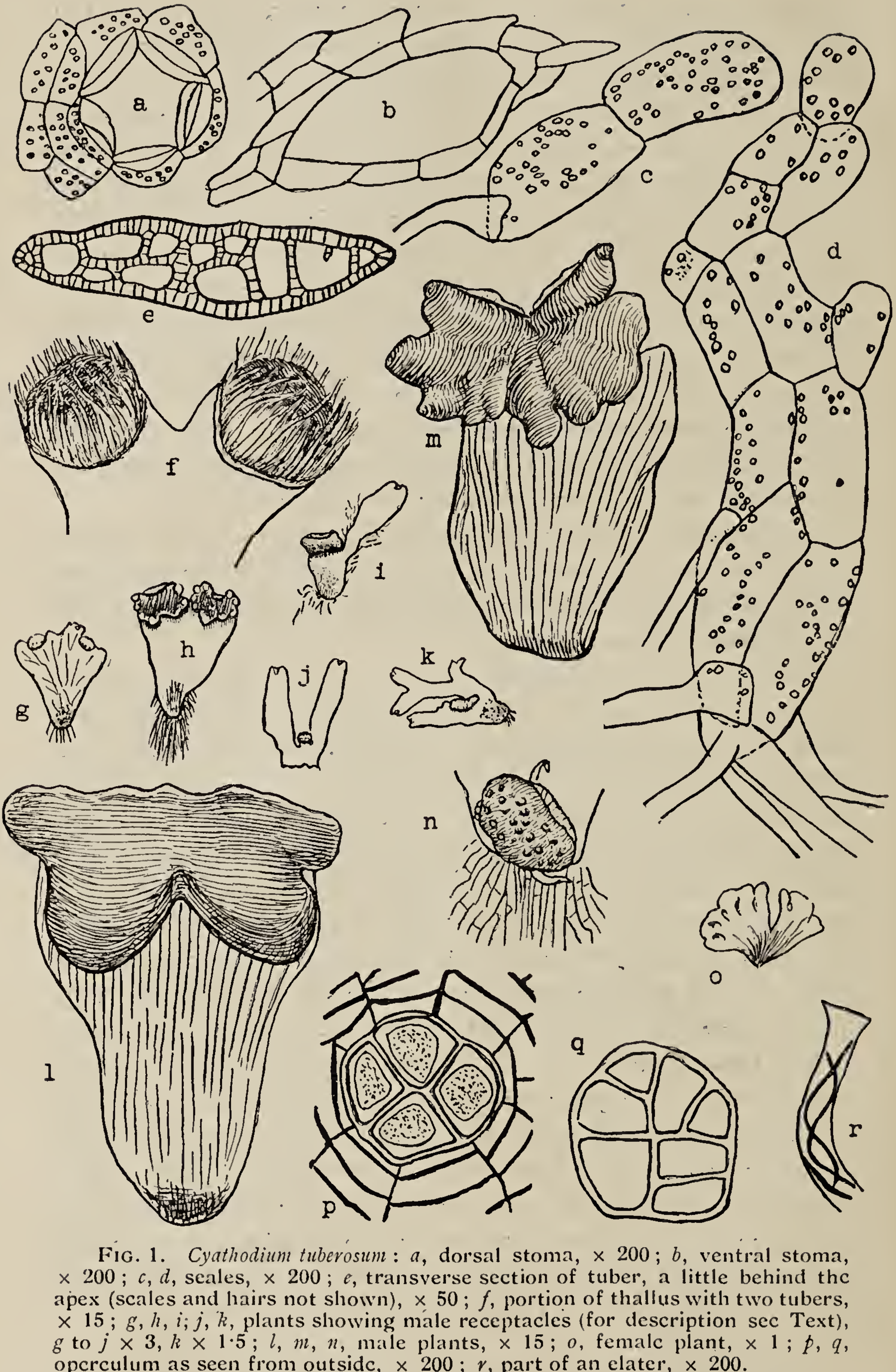


FIG. 1. *Cyathodium tuberosum*: *a*, dorsal stoma, × 200; *b*, ventral stoma, × 200; *c*, *d*, scales, × 200; *e*, transverse section of tuber, a little behind the apex (scales and hairs not shown), × 50; *f*, portion of thallus with two tubers, × 15; *g*, *h*, *i*; *j*, *k*, plants showing male receptacles (for description see Text), *g* to *j* × 3, *k* × 1·5; *l*, *m*, *n*, male plants, × 15; *o*, female plant, × 1; *p*, *q*, operculum as seen from outside, × 200; *r*, part of an elater, × 200.

The growing-point was studied in these tubers and it was found to be occupied by a single initial cell. This cell has a triangular outline in vertical longitudinal sections, and it is oblong in horizontal sections. It cuts off segments dorsally, ventrally and laterally. Goebel[1] concludes from the figures of Leitgeb that a similar apical cell is present in the species investigated by the latter. *C. cavernarum* differs from the present species in having an apical cell cutting three segments (Lang). Vertical transverse sections showed that the tuber was two to four cells thick immediately behind the apical cell, without any spaces between the cells. A little further back spaces appear owing to the more numerous vertical walls in the upper and lower layers and horizontal walls in the middle layers.

C. tuberosum seems to have lost all distinction between its upper and lower surfaces as shown by the position of the pores and the rhizoids. The biological significance of the pores has already been alluded to. The hairs on the upper surface of the tuber protect this region from drought. The part behind the tuber dies in a short time, and often the tuber is separated from the thallus by a constriction before maturity.

The position of the male receptacle is variable, and is similar to the position of the female receptacles of *Exormotheca* and *Aitchisoniella.* It may be terminal, lateral or in the angle between two sterile branches (Fig. 1, *g* to *m*), In the case where it is lateral the main shoot has divided into two branches, one of which grows on as an ordinary branch while the other forms the receptacle. In the case where the receptacle is in the fork the main shoot has divided into two, one of which again forks producing a sterile branch and a receptacle (Fig. 1, *k*). In both cases the receptacle has the form of a cushion separated from the thallus and a little raised by a stalk-like constriction. It is either circular in outline or elongated laterally and has a few scales on the ventral (anterior) side. Where the receptacle is terminal it is much more highly developed. It is raised upon a short stalk-like constriction which has a distinct groove on the anterior surface and is a branch-system. This last form of the receptacle is met with in plants which occur along with large female plants and are often concealed below the latter. In the case of the receptacle being lateral or in the fork branching has occurred, some branches being reproductive, others vegetative. In other plants all branches are reproductive and we have a composite

[1] "Organography of Plants." Eng. Trans., vol. 2, 1905, p. 21.

receptacle consisting of many branches. The same explanation holds good for the female receptacle of *Exormotheca*, but the number of reproductive branches there (two) has become permanently fixed. In *Griffithia*, as described below, the number of female reproductive shoots in an involucre varies between one and two. Finally, in *Targionia* the number is again fixed at one.

Laterally elongated receptacles have also been mentioned by Lang in *Cyathodium cavernarum* and these no doubt indicate a single dichotomy. The terminal receptacles of *C. tuberosum* may have four to nine or more branches (Fig. 1, *h*, *l*, *m*), each being represented by a lobe of the disc and each having a few scales in two rows on the ventral surface. The receptacle is obviously similar to the receptacle of *Marchantia*, but reduced as regards assimilating tissue. Goebel[1] has pointed out that the disc of the receptacle of the composite type like *Marchantia* is not radial but symmetrically divisible only by one plane. This condition is very well seen in the receptacle under consideration (Fig. 1, *h*, *l*, *m*). Antheridia are developed in centrifugal order so that the youngest antheridia are found near the tips of the lobes. The upper surface is studded with the papillæ containing the openings of the chambers in which the antheridia are situated. The mouth of the papilla is usually bounded by six cells. The structure and development resemble what has been described by Lang for *C. cavernarum*. A row of six cells was observed without any vertical walls at one stage of development. The mature antheridium has a short stalk and a wall of large hyaline cells. Ripe spermatozoids were observed in many sections, though the cilia were not visible. The spermatozoids are long narrow thread-like coiled bodies about 10μ long without the cilia. They resemble the spermatozoids of *Targionia hypophylla* and *Riccia crystallina* as observed by the writer, and other Marchantiales in general.

As already stated the female plants (Fig. 1, *o*) are either long and narrow or more often they are fan-shaped, due to rapid dichotomy of the growing-point. Their large size under favourable conditions is remarkable as already mentioned. The number of involucres and sporogonia is very large. In one specimen twenty-one involucres were counted and this is by no means unusual. The number of ripe sporogonia is one to four in each involucre. The archegonia differ in position from those of *C. cavernarum* as the growing-point is displaced downwards and backwards and they come to lie on the lower surface. The involucre is ovoid, opening by a circular or elliptic mouth. An interesting feature in connection with the female receptacle is that after fertilisation stiff short hairs similar to those of the tubers begin to grow from the base, apex and margins of the scales near the involucre, the ventral surface of the involucre and the margins and even the dorsal surface of the thallus for a short distance behind the apex. The number of these hairs is, however, not very large on the dorsal surface.

---

[1] "Organography of Plants." Eng. Trans., vol. 2, p. 85.

The structure of the sporogonium presents some interesting features. The foot and seta are like those of *C. cavernarum.* The former consists of two branched cells and the latter of a row of cells. As usual there is an operculum, a thick-walled region and a thin-walled region in the wall of the capsule. The cells of the latter are full of starch before maturity of the capsule but later on are quite empty. The operculum may consist of four cells in the outermost tier but very often some of these cells divide so that the number is increased to six or seven(Fig. 1, *p*, *q*). One of Griffiths' figures[1] showing a part of the operculum of *C. aureo-nitens* shows clearly that this division also occurs in the latter species. The cells of the innermost tier are not eight as in *C. cavernarum* but sixteen to twenty. They can be easily counted by removing the operculum and examining it upside down. The diameter of the operculum as seen from the outside is about 80μ and the diameter of the whole capsule is 0·5 to 0·75 mm.

The spores have long spinous projections as in *C. cavernarum* with a diameter of 40μ. The spore-mother-cells do not become lobed while undergoing division as is the case in *Targionia hypophylla* mentioned by Cavers[2] and also observed by the writer. The elaters are interesting on account of their shape and position. They are long slender structures, 500 to 550μ long, closely trispiral and have one end expanded and they are fixed to the capsule wall by this broad end (Fig. 1, *r*). Lang[3] describes the elaters of *C. fœtidissimum* as free. Goebel[4] has described similar fixed elaters in species of *Jungermannia.* Griffith[5] figures a part of the capsule wall with one elater partly inside. It may be a mere accident but it is, perhaps, an indication that the elaters are fixed in that species. The number of the elaters is very small. The largest number counted was thirty and the smallest seventeen. They are, however, very regularly placed. The capsule opens by eight valves, and eight elaters are attached near the eight lines of dehiscence at the junction of the thick-walled and thin-walled parts of the capsule wall. The rest are arranged below these towards the base of the capsule at short distances forming eight rows. All the elaters are directed to the centre of the capsule. As the length of an elater is rather more than the diameter of the capsule in its apical and basal part it is probable that they help in the dehiscence of the capsule in addition to the dispersal of the spores by their hygroscopic movements. The small number of the elaters can also be explained by their adhesion to the capsule wall. It would not be easy for a small form like *Cyathodium* to spare material to form numerous elaters, but if the elaters were fixed at one end they would be as efficient as if they were numerous and free.

---

[1] "Icones plantarum Asiaticarum," Part 2, 1849, Plate 69, D. ii.

[2] "Inter-relationships of the Bryophyta," 1911, p. 24 of Reprint.

[3] "Annals of Botany," 1905, p. 420.

[4] "Organography of Plants," vol. 2, p. 99.

[5] "Icones plantarum Asiaticarum," Part 2, 1849, Plate 69, D. ii.

Two abnormalities which are met with in this species may also be described here. (1) In the capsule here and there small clumps of a sticky substance were found in which some abortive spores were imbedded. These masses were often found adhering to the wall of the capsule and appeared as white patches from the outside in spirit material. (2) In one specimen a curious condition was observed. On the ventral surface behind the apex (but not at the apex) of a large fan-shaped thallus some twenty groups of archegonia were found, each group consisting of about six archegonia and seated, it appeared, at the base of a small concave adventitious shoot of the thallus and surrounded by several scales whose cells contained chloroplasts.[1]

It appears from the above that *Cyathodium tuberosum* stands near *C. cavernarum* as regards the structure of the thallus and sporogonium, but it has some peculiarities of its own as for instance, ventral pores, tubers, dioecious habit and fixed elaters among other things. It differs markedly from *C. cavernarum* as regards the male receptacle and the position of the archegonia. The significance of the male receptacle and the position of *Cyathodium* will be discussed at the end of the paper.

TARGIONIA HYPOPHYLLA L. VAR. *INTEGERRIMA*.

The species described there under the above name differs from the type as described by Stephani[2] and others in a few respects, but on the whole it appears that it need not be separated (see footnote below). The chief difference lies in the form of the male receptacle but there are minor differences in the vegetative region as well.

---

[1] Stephani ("Species Hepaticarum," vol. 1, p. 63) has described a similar abnormality in *C. aureo-nitens* where the involucre is replaced by a flat shoot bearing the capsule directly.

[2] "Species hepaticarum," vol. 1, 1900, p. 61.

The plant is very variable as regards its form. In shady moist places where it attains greatest luxuriance it forms masses of deep green overlapping individuals which are fixed only by their bases to the substratum. They are 20 mm. or more long and often dichotomously divided. The scales and the involucre are dark purple. In exposed and moist places the plants grow similarly but have a light-green and even yellowish colour, and are almost always once or twice dichotomously branched. They are, however, smaller, often less than 10 mm. in length. The involucre and the scales are hyaline, or only pink. Often only the appendage of the scale is pink, while the rest of the scale is hyaline. This diminution of colour in the exposed places is surprising. One might have thought that the colour would be deeper. Mucilage cells are usually found projecting from the margins of the scales. In dry and exposed places the plants are firmly fixed to the substratum by the whole of the ventral surface and give off a few straggling branches. In all cases the scales may sometimes be slightly overlapping. There is another difference between the plants in shady and exposed places which concerns the relative size of the spores and elaters. The spores and elaters, in plants growing in shady places are respectively, 30 to 40μ, and 140 to 180μ; whereas in plants found in exposed places they are 25 to 30μ and 180 to 200μ.

The number of archegonia is up to seven in each involucre which may develop one or two ripe sporogonia. The apex of the capsule has short elater-like cells attached to it, but the involucre has no tooth-like interlocking processes as described by Cavers.[1] A few elaters slightly shorter than the normal ones are usually found fixed at the base of the capsule. The seta is very short and the capsule does not come out of the involucre.

The antheridia are found usually on the well known ventral shoots in plants growing in shady places. Each shoot has a cylindrical stalk and a terminal disc studded with antheridial chambers separated by assimilation tissue and possessing numerous scales ventrally. Sometimes, however, these discs develop wings on both sides so that they become terminal and are surrounded by scales on all sides (Fig. 2, *a*, *b*). The scales surrounding these male

[1] "Contributions to the Biology of the Hepaticæ," Leeds and London, 1904, p. 8. (Following a suggestion made by Dr. Cavers, I have given my form the varietal name *integerrima* on account of the entire margin of the involucre).

receptacles are similar to those of the ventral surface, purple in colour, but simpler. The appendage usually is either small or absent. Even more interesting are the variations met with in the male receptacle of plants growing in exposed places. Here the male shoot, though arising from the ventral surface has the appearance of the ordinary shoot, and the antheridia form a cushion along the midrib, but this cushion is not at all separated from the wings of the shoot. In addition to these ventral male shoots in the species under discussion the main shoot itself often forms the antheridial cushion on the midrib (Fig. 2, *c*, *d*). The appearance of these main male shoots is very much like that of the male shoots of some species of *Fimbriaria*. It is interesting to note that in such cases the ventral surface has, at a little distance behind the apex, two rows of scales, but immediately behind the anterior margin the scales sometimes appear to be scattered as in the modified ventral male shoots. The reason of this is that rapid dichotomy occurs and the two or more growing points can often be easily distinguished. But if these growing points were still further obscured, we shall have no indication of the cause of scattered scales. This is what happens in the modified ventral male shoots.

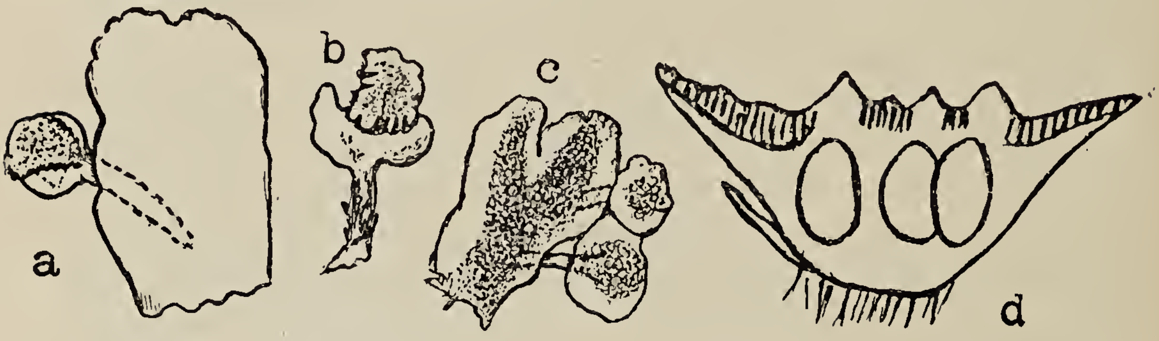


FIG. 2. *Targionia hypophylla*: *a*, *b*, *c*, male shoots, × 4; *d*, transverse section of male shoot, × 20.

It appears, therefore, that the disc of the male shoot of *Targionia* has been formed from a receptacle of a composite type by reduction as described above and as explained by Goebel (Flora, Bd. 101, 1910, Fig. 41). The scales on the ventral surface of each lobe in the ancestral condition would, on the disappearance of the lobes, appear to be scattered on the under surface. The same holds good for the scales surrounding the receptacles of genera like *Plagiochasma* which will be discussed later, especially in view of the species *P. articulatum* in which the receptacles arise terminally but become dorsal by adventitious apical shoots, like those of *Pressia commutata* (Goebel in Flora, Bd. 101, Figs. 19 and 20).

The appearance of the dorsal male receptacle of *Targionia* in exposed places is to be considered a still further reduction. The shoot begins to form vegetative tissue in place of antheridia, so that the latter instead of occupying the whole of the dorsal surface as they do in the modified ventral shoots, occupy only about one half of this. That the disc of the male shoots of *Targionia* is a reduced branch system is further proved by the occurrence of both the composite and the so-called simple receptacle in *Cyathodium tuberosum* where we can actually trace the transformation of the one into the other. In *Targionia* itself there is no trace left of the composite condition except the scattered scales.[1]

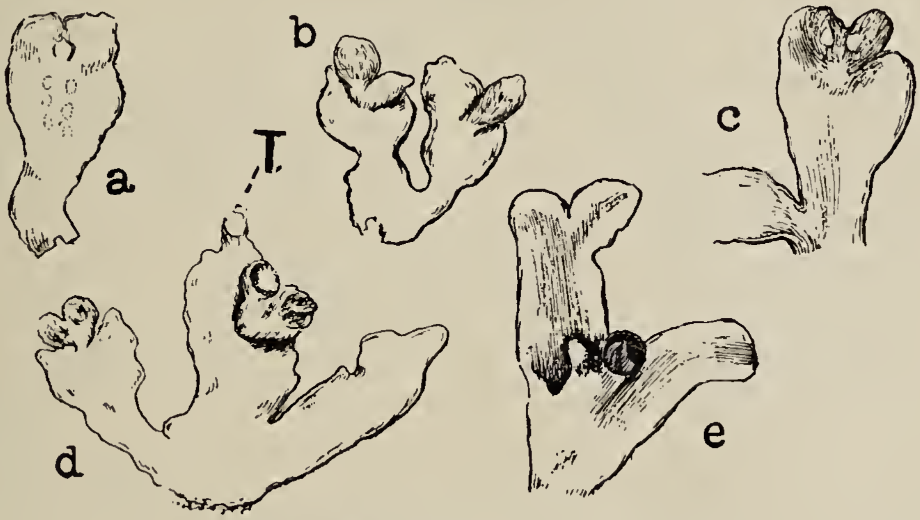


FIG. 3. *Aitchisoniella himalayensis*: *a*, plant with antheridia in two rows behind the female receptacle, × 5; *b*, *c*, *d*, plants showing various positions of female receptacle (*T*, thickened apex), *b* and *d* × 5, *c* × 6; *e*, plant with mature sporogonium, × 5.

AITCHISONIELLA HIMALAYENSIS KASHYAP.

The plants of this species were found growing on an exposed eastern slope only in one locality. They were discovered accidentally near the end of the vegetative season (the end of August). Although a diligent search was made they were not found anywhere else. The number of the plants was, therefore, rather small and almost all of them bore ripe capsules. Fortunately a few young specimens were found among some other liverworts, but it was not known at what particular place in Mussoorie the latter were collected. It is not probable that the species is rare, and the reasons why only a few plants were found are two. First, the search was made at the end of the season when only a few plants would be alive. Secondly, this plant resembles a *Riccia* with which it was found growing and is very small so that it can be easily overlooked or mistaken for the *Riccia*, especially in the sterile state.

---

[1] In this connexion it may be noted that Cavers ("Contributions to the Biology of the Hepaticæ," p. 8) states that the male branches "may give rise to secondary shoots, which may either develop new antheridial receptacles or even grow out as sterile shoots." This observation certainly appears to confirm the view here advanced that the male receptacle of *Targionia* is to be regarded as a reduced branch system.

The thallus is dichotomously divided but sometimes the branches are so placed that the branching appears to be pinnate. The lobes are about 4 mm. long and at most 2 mm. broad, and are oblong-ovate with a small depression at the apex (Fig. 3, *a* to *d*). The plants have a light-green, rather greyish colour. The dorsal surface is perfectly smooth, no raised pores or areoles being visible. The pores, however, are present, being very minute, very little raised, simple and of the type found in the Astroporeæ. Each pore is surrounded by a single ring of six cells which have slightly thickened radial walls (Fig. 4, *a*). The cell walls of the rest of the uppermost layer are quite thin. A thin membrane projects far towards the centre of the pore from the margin (Fig. 4, *a*). The pores are pretty numerous and each leads to an air-chamber below. The chambers have no assimilating filaments and are in one or two layers especially well seen near the margins where the part of the wing forming the floor of the lowermost chamber is reduced to a single layer of cells. The chambers are quite small. They are directed forwards and for this reason a transverse section of the thallus shows several layers of these chambers but a longitudinal section shows mostly a single layer (Fig. 4, *b*, *c*). The ventral surface is hyaline or bluish. The thick midrib projects strongly below and the thallus is continued into the thin wings abruptly as seen at some distance behind the apex; near the apex the midrib gradually passes into the thin margins (Fig. 4, *a*, *e*). The rhizoids are attached to the midrib and are of both smooth and tuberculate kinds. The scales are arranged in two rows on the sides of the midrib so that the latter is not covered by them. They are small, distant, hyaline or bluish and do not project beyond the margins. Each scale is triangular or lunate and has an apical filamentous appendage of three to five cells. The cells of the young scales contain some chloroplasts. The terminal cell of the appendage contains mucilage and similar mucilage cells are also found projecting from the margins, and a few such cells are even found in the body of the scale (Fig. 4, *d*, *e*). Such mucilage cells in the body of the scale have also been observed by the writer in the scales of *Plagiochasma appendiculatum* and *P. articulatum*. The appendage of the scales bends over the growing point and protects it. The cells of the compact part of the thallus contain numerous starch grains. In the older parts of the thallus these cells are either empty or contain some minute grains stained brown with iodine.

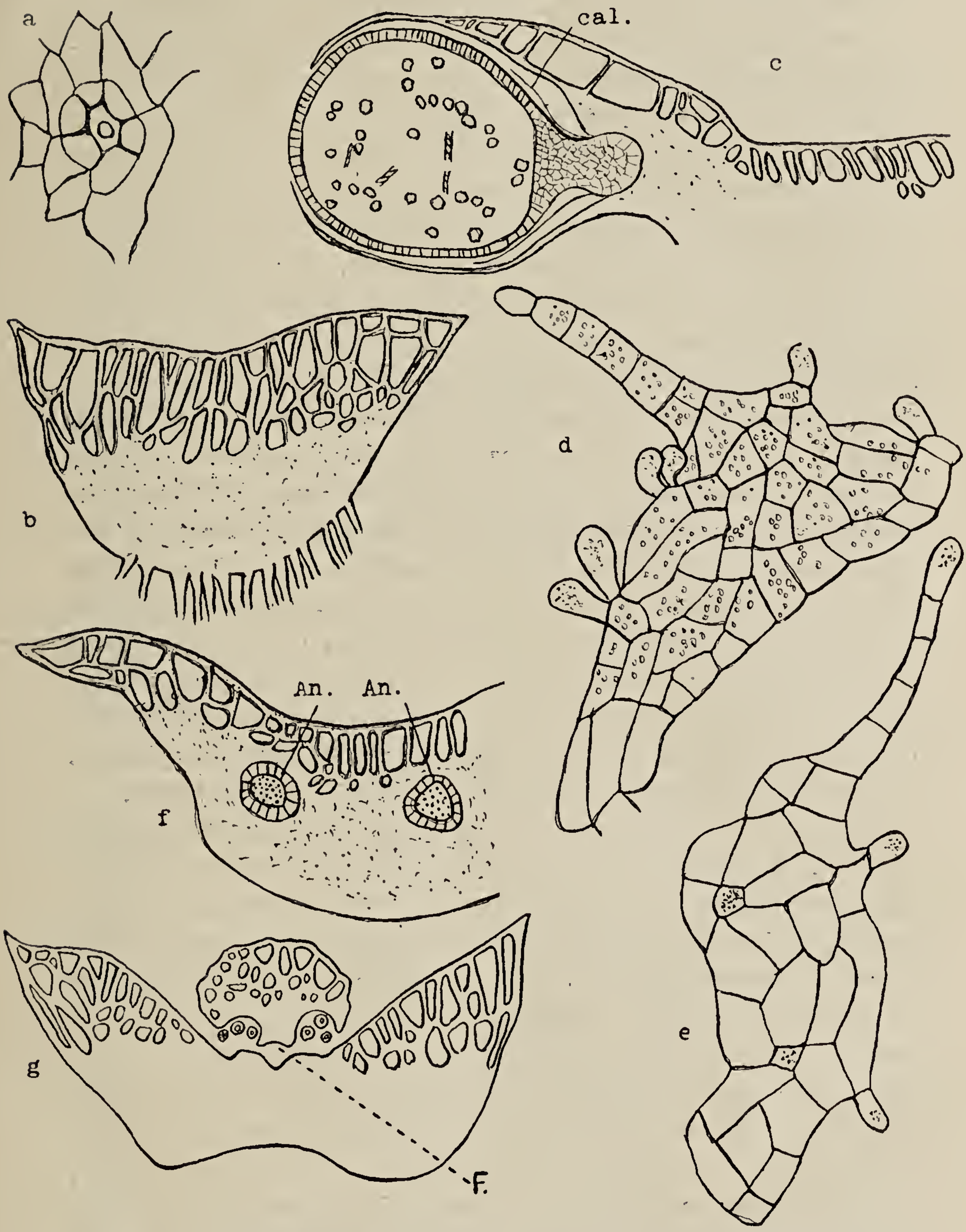


FIG. 4. *Aitchisoniella himalayensis*: *a*, stoma, × 180; *b*, transverse section of thallus near apex, × 40; *c*, longitudinal section of thallus with sporogonium (*cal.*, calyptra), × 40; *d*, scale, × 180; *e*, scale showing mucilage cells (chloroplasts not drawn), × 180; *f*, transverse section of thallus with antheridia (*An.*), × 40; *g*, transverse section of thallus with a female receptacle showing two grooves with archegonia (*F.*, furrow of receptacle), × 40.

We see, on the whole, that the structure of the thallus is like that of a *Clevea*, but the scales are not scattered on the ventral surface. They are in two rows.

The plant is monoecious. The antheridia are produced in two rows embedded in the thallus behind the female receptacle (Fig. 3, *a*). There is absolutely no indication of the presence of the antheridia in the fresh thallus from the outside. There are no projecting papillæ of the antheridial chambers as are found in most other Marchantiales. In spirit specimens the antheridia can be seen by means of a powerful magnifying lens under suitable conditions of light as round white bodies inside the thallus. On account of the small amount of material their development could not be traced. The ripe or almost ripe antheridium lies in close contact with the cells of the thallus and the separation of the thallus cells from the walls of the antheridium can be made out only with difficulty. Even in the microtome sections of the few specimens showing antheridia no trace of a papilla could be made out. Efforts will be made to obtain more material next year in order to work out the development and the dehiscence of the antheridium. The antheridium in the later stages of its development (Fig. 4, *f*) resembles that of *Cyathodium* or *Targionia*. It is, however, not elongated, but spherical and no stalk could be made out. The wall consists of a layer of hyaline cells which were very large and radially elongated in the specimens examined, so that they were very conspicuous. The spermatozoid mother cells did not present any peculiarity.

The female receptacle is very remarkable and variable in position. It may be terminal, lateral or in the fork between two branches (Fig. 3). The position is to be explained in the same way as the position of the male receptacle of *Cyathodium tuberosum*, i.e., some branches of the forking thallus develop as sterile shoots and others become female. The female shoot, however, is reduced to the receptacle. The receptacle may have a single involucre or the shoot may have branched forming two involucres side by side (Fig. 3, *b*). The mature receptacle is attached to the thallus by a small stalk-like constriction which has a distinct groove (Fig. 4, *g*) and a few scales on the anterior (ventral) side. The involucre in the mature state is an ovate body opening by a narrow circular mouth directed upwards and forwards. The dorsal tissue of the receptacle is the same as the dorsal tissue of the thallus and is *continuous* with it. The margins of the involucre are very thin and hyaline and the ventral part is only a single layer of cells in thickness and quite hyaline. The dorsal tissue has the usual pores found in the thallus and similar chambers in one layer directed obliquely forwards.

The receptacle arises as a small hemispherical body at the end of a shoot, but the main shoot, as pointed out before, often forks once or twice before this. The one or two small shoots were seen in several cases near the receptacles about the same level. In this receptacle, if it remains undivided, a vertical groove is present on the anterior surface in which five or six archegonia are produced one after another in one row by the apical cell which can be seen in vertical longitudinal sections below the youngest archegonium. This apical cell in such sections has the usual triangular outline and below it a thin ridge appears a little later which joins the growing margins of the groove. In the meantime the dorsal tissue grows forwards and transforms the groove into a large tubular structure. The archegonial neck consists of six rows of cells. If the receptacle forks and forms two involucres the grooves containing the archegonia are more or less lateral (Fig. 4, *g*).

The resemblance to *Targionia* and *Cyathodium* is obvious. If the shoot which is to form a receptacle, instead of forming the receptacle at once, were to grow a little before producing archegonia we would have a fertile shoot and a receptacle of the type of *Cyathodium* or *Targionia*.

The involucre contained only one ripe capsule in all the specimens examined, but in several cases two or three sporogonia were found in the very early stages. The calyptra is only a single layer of cells. The sporogonium resembles that of *Targionia* (Fig. 4, *c*). The foot is pretty well developed; its cells are densely granular and stain deeply. The seta is short, being a mere constriction between the capsule and the foot. The capsule is wholly like that of *Targionia*. The wall consists of a single layer of cells all of which are strengthened by annular and spiral thick bands. The apex of the capsule has some short elater-like cells with annular bands only attached to it, projecting below into the cavity of the capsule. Three or four short elaters are found fixed at the base of the capsule. Similar cells occur also in the capsule of *Targionia*. The elaters are simple or branched, trispiral and on the average 120μ long. They are fusiform as a rule, but in one case an elater was observed with one end expanded. The spores are 36μ in diameter, tetrahedral, and densely covered with round papillæ on the convex side. The spore-mother-cells do not become lobed at the time of division. The capsule does not come out of the involucre at maturity. It opens by the separation of a part of the apex irregularly.

The chief characters of the genus *Aitchisoniella* may be briefly summarized thus. Thallus of the type of the Astroporeæ, *i.e.*, with narrow chambers in one or two layers and pores with one ring of cells having slightly thickened radial walls; scales in two rows with terminal filamentous appendages; antheridia in two rows along midrib, imbedded in the thallus, behind the female receptacle; female receptacle terminal, lateral or in the fork between two branches, sessile, consisting of one or two involucres joined to the thallus by a stalk-like constriction; dorsal tissue of receptacle continuous with dorsal tissue of thallus; capsule included with a well developed foot; cells of the capsule-wall with thick annular and spiral bands.

It is obvious that the genus *Aitchisoniella* must be placed near *Targionia.* Although the structure of the thallus has some resemblance to that of the thallus in the Astroporeæ, the involucre, the group of archegonia in each involucre, the capsule-wall and to a less extent the ventral scales at once suggest its affinities with *Targionia.* The receptacle in *Aitchisoniella* may bear one involucre or two. In this respect it is midway between *Targionia* and *Exormotheca.* If we suppose the female receptance of *Exormotheca* to become sessile we should have a structure like the female receptacle of *Aitchisoniella* with the difference that the involucres in the latter are not directed so distinctly laterally as those of the former. But this difference can be easily understood by the absence of the peduncle, the small amount of the receptacle-tissue and the stoppage of growth soon after dichotomy. This resemblance between *Aitchisoniella* and *Exormotheca* is further increased if we take into account the position of the female receptacle in the two. We can thus arrange the three genera in a descending series taking into consideration the structure and position of the female receptacle which is admittedly the most important character for classification: (1) *Exormotheca*, (2) *Aitchisoniella*, (3) *Targionia.*

But it might be asked, why should we not arrange them in an ascending series? This, however, cannot be maintained. Apart from the arguments advanced by Goebel after his study of *Monoselenium*, the writer has strong evidence in the structure of *Stephensoniella* and *Plagiochasma articulatum*, which will be described later, that there has been a wholesale reduction in the Marchantiales. At present it is sufficient to call attention to the facts in connection with the male receptacle of *Cyathodium tuberosum.* This genus is undoubtedly reduced and is admitted as such by all. We can see in the species of *Cyathodium* described above the actual reduction of a composite receptacle into a simple disc by the transformation of some of the branches into vegetative shoots and the slight development of the rest so that the margin of the male receptacle does not show any lobes. Indeed, according to this view of wholesale reduction the guiding principle in the evolution of the living Marchantiales has been to increase the amount of vegetative tissue at the expense of the sexual organs and the sporophyte. The writer has already pointed out that in Mussoorie at least reproduction by spores hardly plays any part in the multiplication of the species. The great power of reproducing themselves by vegetative means possessed by all Hepaticæ everywhere indicates that the reproduction by spores in these plants is only of a secondary importance in these days. For this reason the complex receptacles and the complex sporophytes are disappearing and have disappeared in all probability in ancient times.

If a male receptacle can be transformed from a composite type to a simple type as in *Cyathodium tuberosum*, and even such a type again to a mere cushion on the vegetative shoot which is the case in *Targionia*, surely the female receptacle may undergo the same changes, particularly when we find intermediate stages, like the receptacle of *Aitchisoniella*, between *Targionia* and *Exormotheca*. If in *Aitchisoniella* the shoot which is going to form a female receptacle produced at first for some time vegetative tissue, we would have a female branch of *Targionia* type, in which the shoot does not fork and there is therefore only one receptacle. But if the shoot forks, or two or more shoots close to each other behave similarly, we would have a female plant of the type of *Cyathodium tuberosum*. Just as the male receptacle of this species is derived from a composite receptacle by reduction, similarly the female shoot of this plant must have been derived from a composite receptacle possessing many involucres. This view would also explain the fan-shaped appearance of the female plants. We know two involucres are often found in the genus *Aitchisoniella*. Thus *Targionia* and *Cyathodium* may be compared as simple and compound types, while *Aitchisoniella* is intermediate. It is probable, in view of the numerous differences between the two former genera, particularly as regards the sporogonium, that they have arrived at the same structure as regards the female receptacle by parallel evolution. The presence of a composite male receptacle in *Cyathodium tuberosum* along with the facts of the structure of the sporogonium suggests that this genus must have come direct from a high type comparable to *Marchantia*, but now no longer existent. Notwithstanding the great reduction in the thallus of this genus due to its inhabiting dark places, it is still higher than *Targionia* in many respects—for example, the differentiation of the capsule into an operculum, a thickened part and an unthickened portion and its dehiscence by eight definite valves, the tuber-forming habit, and the composite male receptacle.

For this reason in the preceding table (p. 209) giving the relationship of the Marchantiales, *Cyathodium* is shown as descending directly from some *Marchantia*-like ancestor, while *Targionia* is the lowest link in a separate chain of types. The question of the origin of forms like *Corsinia*, *Reboulia*, *Plagiochasma* and *Riccia* will be considered later.

THE MEASUREMENT OF ELECTRICAL CONDUCTIVITY AS A METHOD OF INVESTIGATION IN PLANT PHYSIOLOGY.

By Walter Stiles and Ingvar Jörgensen.

[With Five Figures in the Text].

Introduction.

In this paper an attempt is made to present an account of the work which has been done in regard to the use of electrical conductivity phenomena in the solution of problems of plant physiology. It appears to be desirable to bring together in one paper references to the very scattered literature of the subject, more especially as considerable attention has been devoted to this question recently in various quarters. Further it would seem useful to call attention to the fact that the range of methods available for such work is much wider than is generally supposed ; we have therefore dealt with this aspect of the question, mentioning, as far as we are acquainted with them, the difficulties and advantages and disadvantages of the various methods.

MEASUREMENTS OUTSIDE LIVING TISSUES.

An early attempt to use phenomena of electrical conductivity in the solution of problems connected with plant physiology was made by Heald (16) in 1902. This worker expressed the sap from various plant organs and made measurements of the electrical conductivity of the plant juices so obtained by means of Kohlrausch's well known method. His conclusions were that plant juices are good conductors and that generally the specific conductivity of the sap increases progressively from the root upwards to the shoot. The juice was afterwards incinerated and the ash so obtained diluted to the original volume of the juice; the conductivity of the resulting liquid was then measured. By this means Heald was able to show that the specific conductivity is a rough measure of the relative amounts of mineral substances present in the juice.

Nicolosi-Roncati (27) in 1907, using a method similar to Heald's, also showed the gradual increase of specific conductivity of the extracted juice as one passes from the root upwards. He also measured the freezing point of the juices and showed that there was a rough parallelism between the electrical conductivity and the lowering of the freezing point due to the presence of dissolved substances.

This author also showed that there is a decrease of conductivity of the extracted juice during the ripening of the fruits in the cases of *Arum italicum* and *Solanum laciniatum*. He also tried in one or two cases determining the conductivities of the cortex and stele separately, but no generalisation could be deduced from the results obtained.

The work of Heald and Nicolosi-Roncati has been criticised by Mameli (23), chiefly on two grounds. In the first place she emphasises the wide departure of the conditions of experiment from those in the actual living plant; in this connection she calls attention to the easy alteration in chemical composition to which the extracted juice would be subjected on exposure to air. Secondly she shows that the specific conductivity of the juices will depend largely on the pressure used in extracting the juice. With the rest of this writer's observations we shall deal later on; in regard to the present question she gives figures showing that as the pressure to which the tissues are subjected is increased, so the electrical conductivity of the extracted juice increases. Thus in the case of the apex of the phyllode of *Opuntia Ficus-Indica* the specific conductivity of the expressed sap varied from $108{\cdot}6 \times 10^{-5}$ to $312{\cdot}5 \times 10^{-5}$ according to the pressure used in the juice extraction.

By means of conductivity measurements of the expressed sap, Bouyoucos (9) has been able to show that the quantity of salts present in the sap of wheat seedlings grown in water-culture depends on the concentration of the solution in which the plants were grown. The plant juices were obtained by pressing the seedlings in a mortar until only white fibre was left. The juice was then diluted with distilled water to a definite volume and its conductivity measured.

Recently Dixon and Atkins (10, 11, 12) in a series of investigations on osmotic pressure in plants, have shown that the electrical conductivity of expressed sap increases with increased pressure, thus confirming the result of Mameli mentioned above. They explain this as due to the semi-permeability of the protoplasmic membrane, which allows water to pass out readily, but not the dissolved salts. But with even weak pressure some cells will burst and then sap accordingly passes out and mixes with the water extruded from the compressed but intact cells. With increasing pressure however more cells are broken, and so as the pressure used increases, there increases the concentration of the expressed liquid as regards dissolved substances, and consequently also its electrical conductivity.

So in order to get an extract which shall really represent the sap of the cells it is necessary to render the cell membranes completely permeable before pressure is applied. Chloroform and toluene vapour were made use of for this purpose, but it was found that the most satisfactory method consisted in freezing the tissues in liquid air before pressing out the juice. Much higher numbers were obtained for osmotic pressures and electrical conductivity by this method than had been obtained previously by the same authors. The results of measurements of the conductivity of numerous saps extracted in this way are given by Dixon and Atkins. These results on the whole confirm those obtained by the more inexact methods employed in earlier researches. Thus it was found that the osmotic pressure and electrical conductivity of the sap increases in passing upwards from the root to the shoot. The difference in the conductivity of various saps is considerable, the extremes being a specific conductivity of 1141×10^{-5} for the bases of etiolated leaves of *Apium graveolens*, and 112×10^{-5} for the fruit of *Vitis vinifera*. The latter however had the highest osmotic pressure of all the saps investigated. In fact the low conductivities of organic acids and salts which are abundant in fruits explain the low numbers obtained for the conductivities of fruit saps.

Another group of investigations is that in which the rate of a reaction is measured by means of changes brought about in the electrical conductivity of the liquid in which the reaction is proceeding. This method has been found useful in following enzyme actions in which one of the results of the action is to produce electrolytes where there were none before, or in which the reverse process, the using up of electrolytes to produce non-electrolytes, takes place. The method was introduced for this purpose by Sjöqvist (37) in 1895, and was early made much use of by Oker-Blom (28-31). A brief abstract of such work as has been done on the investigation of enzyme action by means of measurements of electrical conductivity is given by Bayliss (1) in his work on the nature of enzyme action.

Somewhat similar in nature is the work of True and Bartlett (39) on the absorption and excretion of salts by the roots of peas growing in water-culture. These authors obtain a value for the absorption and excretion of salts by roots by measuring the change in electrical conductivity of the solutions in which the plants are growing. Their measurements are made by Kohlrausch's method.

MEASUREMENTS IN LIVING PLANT TISSUES.

In measuring the conductivity of living tissues one is of course dealing with a much more complex and difficult matter than in the case of "in vitro" measurements. The first measurements of this kind of which mention may be made are those of Pollacci (36). This worker, in experimenting on the effect on photosynthesis of the passage of an electric current through an assimilating leaf, has incidentally measured the currents he used. The current was a direct one given by a battery of low E.M.F., *e.g.*, two Daniell cells, and was measured by a D'Arsonval galvanometer. The current was passed through the leaf from the stalk to the tip, or in the reverse direction; the electrodes used were presumably either those of Du Bois-Reymond or those described by Pollacci earlier in the same paper, as consisting of modifications of the so-called non-polarisable electrodes of D'Arsonval, which were held in contact with the leaf by means of wooden pincers. A number of leaves were experimented upon by Pollacci in this way, and in each case the resistance was measured at intervals for a varying number of hours, and curves plotted between current and time. With the alleged effect of the current we have not to deal at present; what we have to notice here is that in all cases there was observed a gradual diminution of the current, although generally there was a rise for a short time early in the second day of observation. Except for this the fall appeared quite regular. Thus in one case the current decreased from 2·38 microamperes to 0·10 microamperes in 56½ hours. Similar results were obtained in all other cases.

Some direct attempts at measuring the conductivity of living plant tissues have been made by Mameli (23). Her method consists in immersing platinum electrodes of various shapes in the tissues of the plant, and measuring the resistance between them by means of an alternating current and Hartmann and Braun's modification of the telephone-bridge arrangement of Kohlrausch. Although no distinct minimum of vibration could be made out in the telephone for the first fifteen minutes, yet after that time a distinct minimum could be discerned and the resistance measured. By this method the author was able to make out that as leaves detached from the plant undergo slow drying the specific conductivity at first diminishes, then it rises again, and in some cases passes the value of the specific conductivity of the attached leaves. She found also that the specific conductivity of a plant organ decreases as the organ gets older. This result she imagines can be explained by the increase in quantity of ash constituents in the leaves as they get older, and consequently in the decrease of ionisation. It is necessary on this view, she adds, to imagine that outside the ash constituents, all other substances, both ionised and non-ionised remain constant. Finally in two cases examined, she found the specific conductivity at the base of the leaf was greater than at the apex.

Stone and Chapman (38) have published some measurements of the electrical resistance of trees. Their method consisted in driving galvanised iron nails about three inches long into the wood of the trees. These served as the electrodes and were in some cases 10 feet, in other cases 8 feet apart.

The trees experimented upon were the sugar-maple (*Acer saccharum* Marsh) and the American elm (*Ulmus americana* L.). The current used was apparently a direct one as it was measured by a galvanometer. It was only used for measuring the resistance and did not flow in between the measurements. Stone and Chapman interpret their results as showing that the resistance depends on the temperature—the higher the temperature the less the resistance. The average resistance is highest on the north side of the tree, followed by the west, south and east sides. This they suppose is correlated with the temperature, which is least on the north side, followed by the west, south and east.

The flow of sap appears to exert no influence on electrical resistance of trees ; nor, other than temperature, do meteorological factors, such as relative humidity, pressure, or winds.

It should be noted that in these observations a wide range of resistance was noted ; for instance the resistance measured on the south side of the tree varied from 18,000 ohms to 53,900 ohms. Taking this variation into consideration it seems very doubtful whether the differences of the mean resistance of different sides of the tree, which were only 5 per cent. between north and south, and 8 per cent. between east and west, have any meaning.

By measurement of the resistances of ringed and unringed cut branches it would appear that the cambium offers the least electrical resistance ; this is followed by the phloem and sap wood.

The same writers also made some measurements with herbaceous plants ; the species used was the Tobacco (*Nicotianum tabacum* L.). The platinum electrodes were 14 inches apart. Here again rather wide variations in resistance were noted which could not generally be correlated with temperature. Thus at 60°F. two measurements in the same experiment were 108,000 ohms and 150,000 ohms, a difference of more than 30 per cent. of the mean of the two readings.

The most noteworthy work that has yet been done on the living plant in which conductivity measurements are made is that of Osterhout (32, 35) on the permeability of protoplasm to ions. In this work discs of *Laminaria* were cut out with a cork borer, and 100 to 200 of them were packed closely together so as to form a cylinder. This cylinder was immersed in sea water and other liquids and was kept in place by means of glass rods. At each end of the cylinder was a block of hard rubber containing a platinum electrode. The measurements were made by Kohlrausch's method. The resistance of the cylinder of tissue in sea water was 1,110 ohms and when killed it fell to 320 ohms.

When this cylinder of tissue was placed in various solutions it was possible to show the rate at which the ions in sodium chloride or other electrolytic solution entered into the tissue by the rate at which the resistance fell from 1,110 to 320 ohms. When solutions of sodium chloride and calcium chloride were mixed in a certain proportion it was found that the resistance remained unaltered for twenty-four hours. This was attributed to the antagonistic action of the salts on one another, both sodium and calcium ions being prevented from entering. Sea water is also such a "balanced" solution.

In a further series of experiments in which the same method was used, Osterhout (33) has shown that electrolytes may produce a reversible change in permeability of the cell.

A third series of experiments (34) was made by the same writer with a view to determining the effect of anæsthetics upon permeability. It was found that below a certain concentration of the anæsthetic a decrease in permeability is produced which is reversible; above a certain concentration of anæsthetic the decrease in permeability gives place rapidly to an increase in permeability which is due simply to toxic action and is not reversible: with further increase in concentration of the anæsthetic the preliminary period in which there is a decrease in permeability becomes so momentary as to be undetectable. Thus with anæsthetic action is associated a decrease in permeability of the protoplasm, the later increase in permeability which is observed with higher concentrations of the anæsthetic is common to the action of all toxic substances.

REVIEW OF THE METHODS APPLICABLE FOR CONDUCTIVITY MEASUREMENTS IN LIVING TISSUES.

In the preceding sections of this paper we have given a review of the work that has been already done in the direction of making use of electrical conductivity measurements in questions of plant physiology. This review is probably not complete; in any case however it enables us to form an idea of the work that has been done, and gives us a basis for reviewing the methods which are available for further work based on the same underlying principles of method.

In regard to measurements outside the plant, we have little to say here. Such measurements can be little different from those of ordinary electrolytes and present little difficulty compared with the measurement of conductivity in living tissues, which would seem a much more important thing to do satisfactorily. It is then more especially with the methods applicable to such measurements that we propose to deal in this section of our paper.

The difficulties of using direct currents for such measurements are well known. Polarisation effects are produced at the electrodes, and these effects are more marked the smaller the surface of the electrodes. Now in such experiments as are involved in the subject we are considering it would seem generally necessary to use small electrodes of thin platinum wire which can be immersed in the plant. It is only by immersion of the electrodes in the tissues that a good contact can in any way be assured, and many plant organs are too small to admit of any larger electrodes than platinum wire. It has moreover to be observed that in the case of immersion the larger the electrode the greater will be the quantity of wounded tissue.

The value of so-called unpolarisable electrodes is very doubtful in the case of living tissue as polarisation effects are probably not only produced at the metallic electrodes, but everywhere in the plant where there is a surface of junction of two immiscible phases.

Further in the case of the direct current there will take place electrolysis of substances inside the plant resulting in the formation of substances inside the cell. There will be also a probable increase in concentration of electrolytes about the electrodes; and not an increase in concentration of electrolytes only: it is probable that colloidal substances and other non-electrolytes will also be transported to the electrodes (electrokinesis).[1] It is probably due to such changes as these that a continuous direct current as small as 10 microamperes will often kill a plant in a few hours.

It is possible however that the method of using a direct current may be of use in preliminary experiments, especially when the action under consideration produces an effect on the conductivity that is the reverse of that produced by the electrode and other effects of the direct current. Some preliminary experiments of the authors may serve to indicate this.

The general result of the complications at the electrodes is to produce a rather regular and rapid increase in the resistance, which is slower the greater the E. M. F. used (provided of course the original resistance is the same). This is indicated by the following curves (Fig. 1).[2]

When a stem with a direct current passing through it is chloroformed the result is a rise in conductivity as is indicated by the following curve (Fig. 2). There can be no doubt of the general result of the action under consideration as both the electrode effects and the presence of the non-electrolyte chloroform would favour a change of the conductivity in the opposite direction.

It may also be possible to use the method if the E. M. F. used and the resistance are both large, when it is only necessary to use the current momentarily to take a galvanometer reading, as has been done by Stone.

[1] See, *e.g.*, Bernstein (2).

[2] Cf. Pollacci (36).

Also it should be noted that the electrolytic effect is much reduced when very small currents are used. As it is possible to measure currents of the order of 10^{-14} amperes, the use of such low direct currents might be possible for some determinations.

But the use of an alternating current is much to be preferred. By introducing and elaborating the method of using alternating currents in the determination of electrolytic resistances Kolrausch rendered a great service to physical science. His method is so well known as to need no description here; descriptions are to be found in many physical text-books. This is the method that has been almost exclusively used in the case of conductivity measurements of sap-extracts and of other liquids outside the plant, and is no doubt quite satisfactory for the purpose.

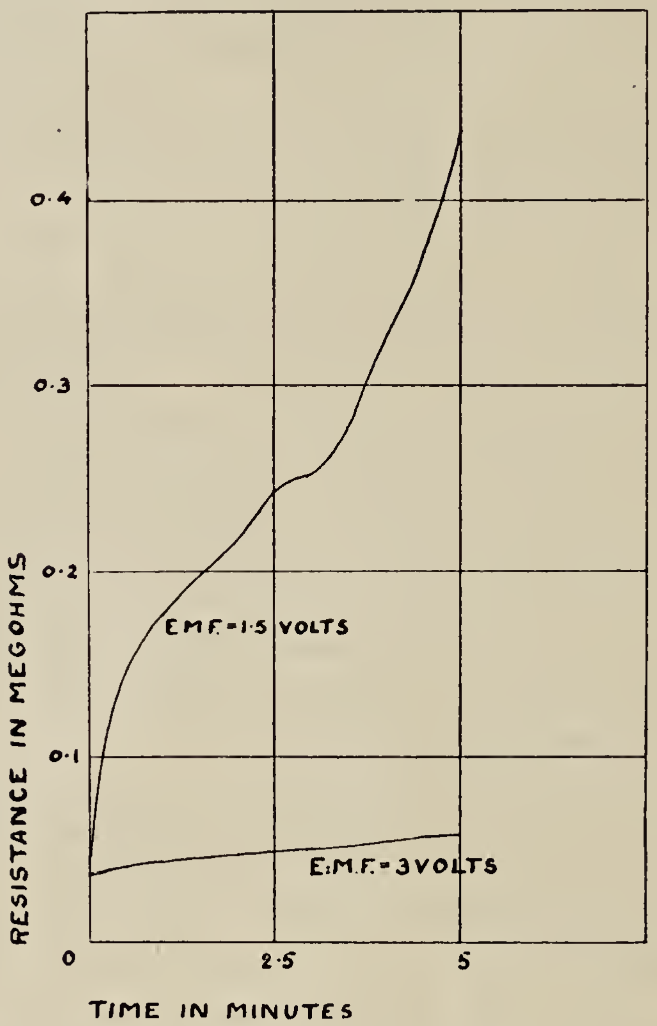


FIG. 1. For explanation see text.

In the case of living tissues, however, Kohlrausch's method is unsuitable for several reasons. In the first place, as Kohlrausch himself points out, it is necessary to have electrodes of a certain size. Indeed the area of surface of the electrodes is an important factor in obtaining correct results with this method. In the second place, in dealing with large resistances such as one meets with in living tissues, it is difficult to discern the minimum in the telephone. Thirdly, it takes some little time to make a measurement by Kohlrausch's method, and so it is inconvenient when one wants to get a continuous record of a changing conductivity.

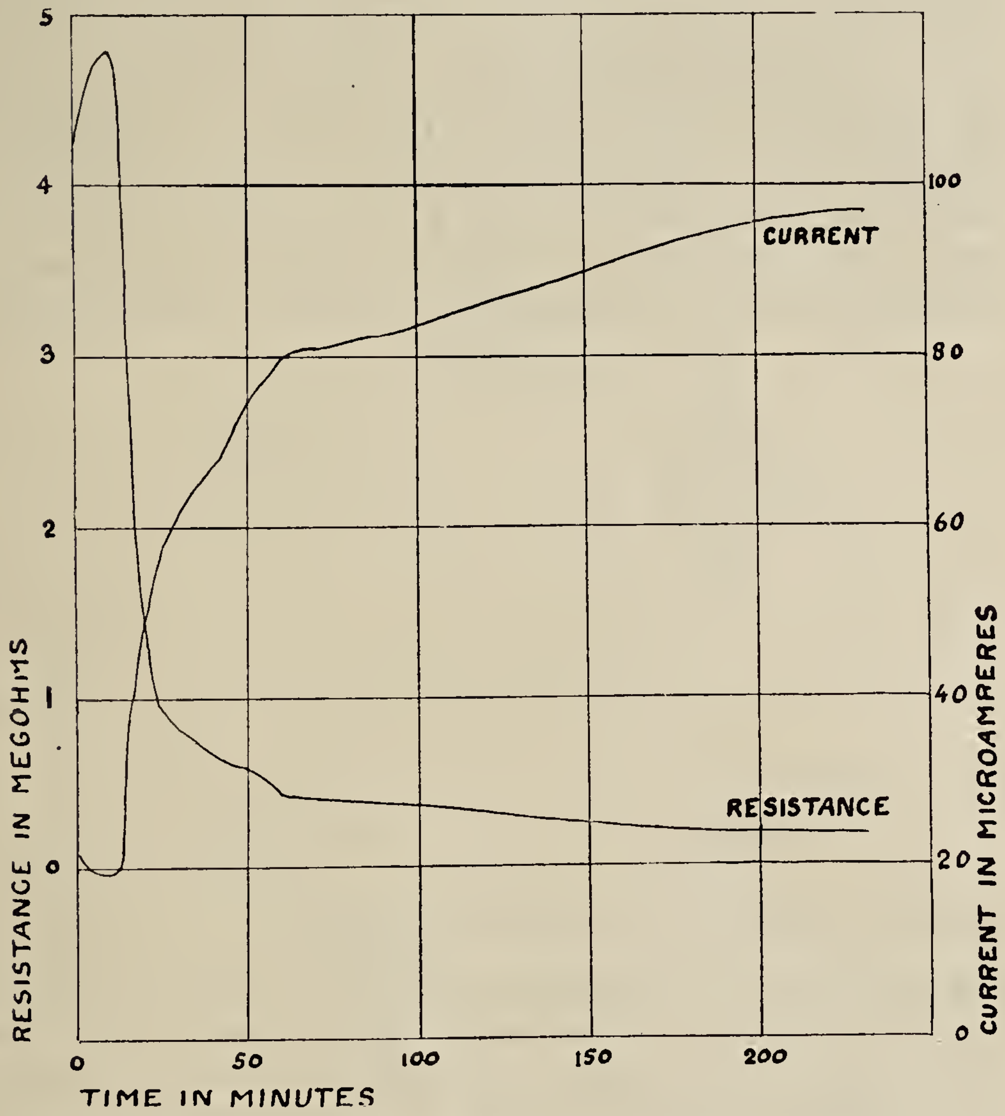


FIG. 2. Diagram showing the decrease of resistance of a stem of *Tradescantia* when treated with chloroform ten minutes after the commencement of the experiment.

A method which is less known is that first described by Fitzpatrick (14) and later elaborated by Whetham (40), and which has also been described by McIlhiney (24).

In this case a direct current is alternated by a commutator before it passes through an electrolytic resistance. The current is then passed through a second commutator rotating synchronously with the other, so that it is made direct again before it is passed through a galvanometer. The sketch of the connections will make the arrangements clear (Fig. 3).

In his own experiments Whetham used a Wheatstone's bridge arrangement, measuring his resistance by comparison with standard resistances as in Kohlrausch's method. Whetham himself experienced various difficulties, which he endeavoured to surmount. Thus as regards the electrodes he found bright platinum gave good results with extreme dilution, but a too high resistance in other cases. On covering the electrodes with platinum black the results were variable, the platinised electrodes extract salt from the solution and deposit it on their surface. After heating the platinised electrodes red hot it was found possible to measure resistances varying from 10 to 50,000 ohms with an accuracy of 1 per cent. Other possible difficulties arise from the winding of the coils in the resistance box, which might give rise to errors due to their capacity and self-induction; and also from the thermo-electric force between the revolving drum and the brushes of the commutators. The thermo-electric force however does not give rise to any serious error, while any error due to winding of the resistances can of course be eliminated by using suitably prepared resistances.

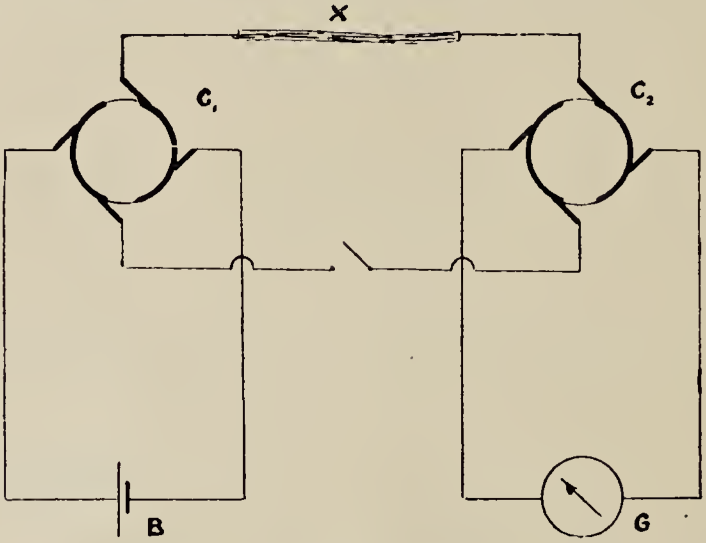


FIG. 3. For explanation see Text. B, battery; C_1, C_2, two commutators rotating synchronously; G, galvanometer; X, resistance.

So far this method has only been used to compare resistances; it would be better to apply a method that would measure the resistance or conductivity absolutely than one which merely compares resistances. This would avoid capacity and induction effects in the standard resistances, and owing also to the simplification of the method, should enable a continuous record to be made.

Our own attempts in this direction with the revolving commutator method indicate that great difficulty arises in trying to keep a constant contact between the brushes of the commutator and the revolving drums, a difficulty which has also been emphasised recently by Hammer (15).

A second method in which the same principle is used, namely, passing an alternating current through the electrolyte and rectifying it when passing it through the measuring instrument, is described by Morgan and Hildburgh (25). Their arrangement is indicated in the accompanying diagram and description (Fig. 3), from which it will be perceived that this method is also, though in a different way, one in which the unknown electrolytic resistance is compared with standard resistances, and which is therefore open to the same errors as the method of the revolving commutators. Morgan and Hildburgh describe a modification of the method by which the measuring instrument can be standardised, but they describe it as not so accurate a way as that in which the resistances are compared.

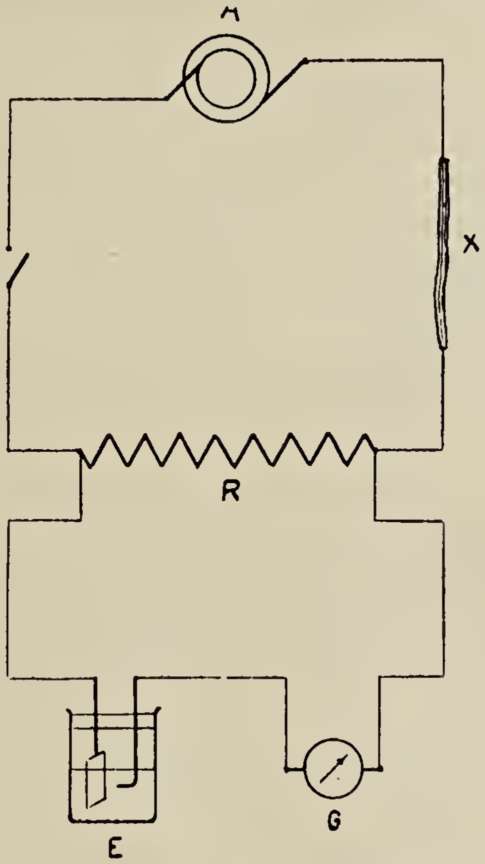


FIG. 4. Diagram to illustrate the arrangement of Morgan and Hildburgh (see Text). An alternating current generated at A passes through the electrolytic resistance X. R is a large ordinary Ohm's resistance. The current measuring instrument G is put in series with the electrolytic rectifier E and so measured as a direct current. The electrolytic resistance is measured by replacing X with standard resistances which give the same deflection of G.

Simpler than any of the methods so far described would be the use of an instrument for measuring as such the alternating current actually passing through the electrolyte. One would then know definitely what was happening as regards the conductivity, and one would also be able to follow any changes continuously. Moreover such a method would require a much less complicated arrangement of apparatus. It would also allow working with a frequency of alternation in which polarisation would be negligible, such as one cannot reach with the commutator method. During recent years development in instrument-making technique has resulted in the production of such simple and reliable instruments for measuring even small alternating currents, such as Duddell's Thermo-Galvanometer made by the Cambridge Scientific Instrument Company. Along such a line as this probably more numerous and more reliable results may be expected than those obtained hitherto.

ON THE PASSAGE OF ELECTRIC CURRENT THROUGH LIVING TISSUES.

In the preceding part of this paper we have described the methods available for measuring the electrical conductivity of living plant tissues, and we have emphasised the advantage of using a method which will provide us with a continuous record of the conductivity. It is therefore necessary to consider the phenomena that accompany the passage of the current through part of a living plant.

In the case of living tissues we are of course dealing with a very complicated state of affairs, far removed from the relatively simple conditions which exist in the passage of a current through a solution of a single electrólyte. We have a large number of living cells separated by cell walls of dead material, and we have first to consider the possibility of the currents passing through the walls alone and avoiding the cells altogether.

However there seems to be no doubt that the living cells do actually act as conductors, as is indicated by the very voluminous literature dealing with the effects of electric current on cell contents.[1] Each cell is however a very complicated system. It contains the cell-sap, which may consist of a solution of a variety of electrolytes and non-electrolytes, as well as the actual protoplasm which is separated by its limiting membrane characterised by its well-known so-called semi-permeable properties. Thus a change in conductivity may be due to alteration in the concentration of electrolytes or non-electrolytes in the cell-sap, or possibly to changes in the protoplasm, or to changes in the permeability of the protoplasmic membrane.

---

[1] See, *e.g.*, Klemm (19) and Ewart (13).

Yet a further complication becomes obvious when we consider the so-called bio-electric phenomena in plants. These bio-electric phenomena have been much studied since Galvani's famous experiments but in spite of a very voluminous literature dealing with these questions, little is really known about them. Recent work, more especially that of Nernst (26) and Beutner (3-8) and Loeb and Beutner (20-24), appears to throw more light on the subject. From the work of these authors it seems reasonable to regard living tissue as analogous to a complex of galvanic cells, and which should therefore behave in a similar way to the latter when a current is passed through them.

The recent work of Höber (17, 18) has however indicated methods by which these phenomena may be eliminated, and enable us to obtain information regarding the interior of the cells.

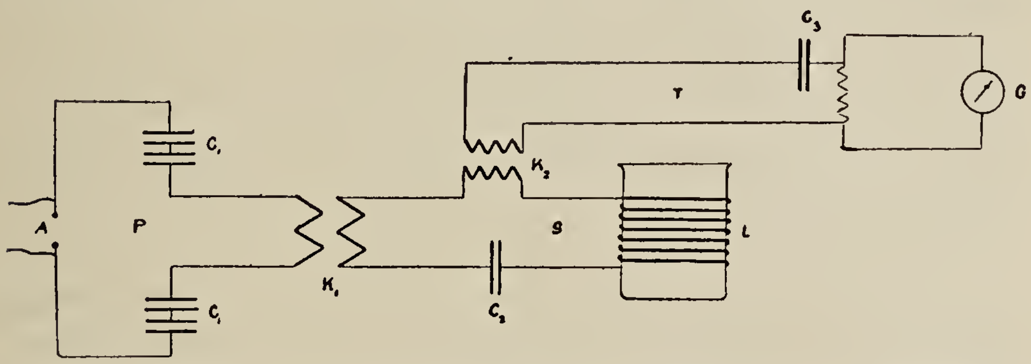


FIG. 5. In the primary circuit *P*, *A* is the spark gap of an induction coil; C_1, condensers; *K*, the coupling coil which couples the primary circuit to the secondary circuit *S* containing the capacity C_2 and self-induction *L*, in which is placed as core the vessel containing the electrolyte. *T*, the tertiary circuit containing the measuring instrument *G*.

Höber's work is based on the assumption that living cells possess a considerable internal conductivity, *i.e.*, that a considerable part of the salts contained in them must be present as free salts. As however the passage of a current through a system of cells will be accompanied by polarisation at the surface of junction of two phases, the ordinary methods do not give any information regarding the conditions in the interior of the cell. The method used by Höber involves the use of waves instead of a low-frequency alternating current. Various modifications have been used, the development of the methods being quite a unique example of adaption of physical science to physiological purposes. The principle involved in one of Höber's earlier methods consisted in the production of waves in a circuit containing self-induction and capacity. The damping of the waves which was produced by using a suspension of cells as core in the self-induction was measured.

Fig. 5 will give an idea of the general arrangement. The frequency of the waves was of the order 10^6–10^7. By comparing this damping effect with that produced by electrolytes of various concentrations, Höber determines the internal conductivity of the cell.

In later experiments better results were obtained by measuring the damping effect when the electrolyte or cell-suspension was introduced into the capacity or into a small capacity in parallel with the main one. In the latest development of the method the damping electrolyte was placed in parallel with the self-induction, and was contained in a glass tube with platinum electrodes.

Höber's measurements indicate that the internal conductivity of the cells examined is much greater than the conductivity measured by Kohlrausch's method. The internal conductivity is not altered by the addition of the non-electrolyte saponin, whereas the addition of this substance increases the conductivity as measured by Kohlrausch's method. This indicates that the cell-surface must constitute an obstacle to the diffusion of the ions, *i.e.*, there must be a plasma-membrane, which before the addition of the saponin is only to a certain extent permeable to the ions.

Höber's work has been done with suspensions of blood corpuscles and with animal tissues. It would be interesting to see what would be the result of the application of his methods to plant physiology.

CONCLUSION.

From these pages it will be seen that the use of electrical conductivity methods in plant physiology is still only in its preliminary experimental stage. Having regard to the results which have so far been obtained by its means it seems likely that with further development of methods, electrical conductivity will afford a convenient and comparatively simple means of investigating certain classes of problems in plant physiology.

THE UNIVERSITY.
LEEDS.
25th February, 1914.

LITERATURE CITED.

1. Bayliss, W. M. "The Nature of Enzyme Action." Third Edition, London, 1914.
2. Bernstein, J. "Elektrobiologie." Braunschweig, 1912.
3. Beutner, R. "Potential Differences at the Junction of Immiscible Phases." Trans. Amer. Electrochem. Soc., Vol. 21, 1912, p. 219.
4. ,, "Die physikalische Natur bioelektrische Potentialdifferenzen." Bioch. Zeitsch., Bd. 47, 1912, p. 73.
5. ,, "Water-Immiscible Organic Liquids as Central Conductors in Galvanic Cells." Trans. Amer. Electroch. Soc., Vol. 23, 1913, p. 401.
6. ,, "New Galvanic Phenomena." Amer. Jour. Physiology, Vol. 31, 1913, p. 343.
7. ,, "Neue Erscheinungen der Elektrizitätserregung, welche einige bioelektrische Phänomene erklären. Erster Teil." Zeitsch. für Elektrochemie, Bd. 19, 1913, p. 319.
8. ,, "Neue Erscheinungen der Elektrizitätserregung, welche einige bioelektrische Phänomene erklären. Zweiter Teil." Ibid., Bd. 19, 1913, p. 467.
9. Bouyoucos, G. "Transpiration of Wheat Seedlings as affected by different Densities of a Complete Nutrient Solution in Water, Sand and Soil Cultures." Beihefte zum Bot. Centralbl. Bd. 29, Abt. 1, 1912, p. 1.
10. Dixon, H. H., and Atkins, W. R. G. "Osmotic Pressure in Plants. I. Methods of Extracting Sap from Plant Organs." Sci. Proc. Roy. Dublin Soc., Vol. 13, (N.S.), 1913, p. 422.
11. ,, ,, "Osmotic Pressure in Plants." II. Cryoscopic and Conductivity Measurements on Some Vegetable Saps." Ibid., Vol. 13, (N.S.), p. 434, 1913.
12. ,, ,, "Osmotic Pressure in Plants. III. The Osmotic Pressure and Electrical Conductivity of Yeast, Beer and Wort." Sci. Proc. Roy. Dublin Soc., Vol. 14 (N.S.), 1913, p. 9.
13. Ewart, A. J. "Protoplasmic Streaming in Plants." Oxford, 1903.
14. Fitzpatrick, T. C. "On the Application of Alternating Currents to the Determination of the Conductivity of Electrolytes." Brit. Ass. Report, 1886, p. 328.
15. Hammer, W. "Ueber einen neuen Stromwerden." Phys. Zeitschr., Bd. 13, 1912, p. 948.
16. Heald, F. de F. "The Electrical Conductivity of Plant Juices." Bot. Gazette, Vol. 34, 1902, p. 81.
17. Höber, R. "Ein zweites Verfahren, die Leitfähigkeit im Innern von Zellen zu messen." Archiv für die ges. Physiologie, Bd. 148, 1912, p. 189.
18. ,, "Messungen der inneren Leitfähigkeit von Zellen. Dritte Mitteilung." Ibid., Bd. 150, 1913, p. 15.
19. Klemm, P. "Desorganisationserscheinungen der Zelle." Jahrb. f. wiss. Bot., Bd. 28, 1895, p. 627.
20. Loeb, J., and Beutner, R. "On the Nature and Seat of the Electromotive Forces manifested by Living Organs." Science, Vol. 34 (N.S.), 1911, p. 884.
21. ,, ,, "Die Bedeutung der Lipoide für die Entstehung der bioelektrischen Potentialdifferenzen bei gewissen pflanzlichen Organen." Bioch. Zeitsch., Bd. 51, 1913, p. 288.

22. Loeb, J., and Beutner, R. "Einfluss der Anæsthetica auf die Potentialdifferenz an der Oberfläche pflanzlichen und tierischer-Gewebe." Bioch. Zeitsch., Bd. 51, 1913, p. 300.

23. Mameli, Eva. "Sulla conducibilità elettrica dei sucche e dei tessuti vegetali." Att. dell' Ist. Bot. dell' Università di Pavia, Ser. 2, Vol. 12, 1909, p. 285.

24. McIlhiney. Jour. Amer. Chem. Soc., Vol. 20, 1898, p. 206.

25. Morgan, J. L. R., and Hildburgh, W. L. "A method for the Determination of Electrical Conductivity with Direct Current Instruments." Jour. Amer, Chem. Soc., Vol. 22, 1900, p. 304.

26. Nernst, W. Archiv. f. d. ges. Physiologie, Bd. 122, 1908, p. 307.

27. Nicolosi-Roncati, F. "Ricerche su la Conduttività elettrica e la pressione osmotica nei vegetali." Rend. della R. Accad. delle Sci. Fis. e Mat. di Napoli, Fasc, 12, 1907.

28. Oker-Blom, M. "Thierische Säfte und Gewebe in physikalisch chemischer Beziehung. Sechste Mettheilung. Die elektrische Leitfähigkeit und die Gefrierpunktserniedrigung als Indicatoren der Eiweisspaltung." Skand. Archiv. fur Physiologie, Bd. 13, 1902, p. 359.

29. ,, "Thierische Säfte und Gewebe in physikalisch chemischer Beziehung. Siebente Mittheilung. Zur Frage von den autolytischen Erscheinungen in Blutserum und Muskelsaft." Ibid., Bd. 14, 1903, p. 48.

30. ,, "Bestimmung der elektrischen Leitfähigkeit mit Bezug auf bakteriologische Zwecke." Centralbl. für Bakt., Bd. 37, 1904, p. 150.

31. ,, "Die elektrische Leitfähigkeit im Dienste der Bakteriologie." Zentr. Bact., Bd. 65, 1912, p. 382.

32. Osterhout, W. J. V. "The Permeability of Protoplasm to Ions and the Theory of Antagonism." Science, Vol. 35 (N.S.), 1912, p. 112.

33. ,, "Reversible Changes in Permeability produced by Electrolytes." Science, Vol. 36 (N.S.), 1912, p. 350.

34. ,, "The Effect of Anæsthetics upon Permeability." Science, Vol. 37 (N.S.), 1913, p. 111.

35. ,, "Some Quantitative Researches on the Permeability of Plant Cells." The Plant World, Vol. 16, 1913, p. 129.

36. Pollacci, G. "Eletricità e Vegetazione." Atti dell' Ist. Bot. della R. Università di Pavia, Vol. 13 (N.S.), 1907.

37. Sjöqvist, J. "Physiologisch-chemische Beobachtungen ueber Salzsäure." Skand. Arch. für Physiologie, Bd. 5, 1895, p. 277.

38. Stone, G. E., and Chapman, G.H. "Electrical Resistance of Trees." Twenty-fourth Annual Report of the Mass. Agric. Exp. Sta., 1912.

39. True, R. H., and Bartlett, H. H. "Absorption and Excretion of Salts by Roots, as influenced by Concentration and Composition of Culture Solutions. I. Concentration Relations of Dilute Solutions of Calcium and Magnesium Nitrates to Pea Roots." U.S. Dept. of Agric. Bureau of Plant Industry Bull. No. 231, Washington, 1912.

40. Whetham, W. C. D. "On the Ionisation of Dilute Solutions at the Freezing Point." Phil. Trans. Roy. Soc. London, Vol. 194, 1900, p. 321.

NOTE ON THE BIOLOGY OF *FEGATELLA CONICA.*

BY ANNIE C. MAYBROOK.

[WITH ONE FIGURE IN THE TEXT].

THE following investigation of variation in the thallus structure of *Fegatella conica* was carried out on plants found, during July, 1913, growing in a small hole in a high hedge bank, near Wetton in Derbyshire. The hole was broad-mouthed, narrowing at the back where there was a continuous dripping of water. It was thickly overgrown inside with plants of a thalloid liverwort (which proved to be *Fegatella conica*) also present on the bank around the hole. The plants shewed great variation in form and size of the thallus, and in the number of spots, which indicated the position of the air chambers.

The light intensity was measured at different positions in the cavity by means of Wynne's exposure meter. Samples of thalli were taken from these positions, and later on their structure was investigated. In none of the forms were any sexual organs present, but the flask-like form of the assimilating filaments was sufficient to identify the liverwort as *Fegatella conica*. The light intensities at the different positions were expressed as fractions of the total daylight outside the cave, which was taken as unity.[1] These fractions will be referred to as the fractional light intensities at the different positions. Forms of thalli will be referred to as Forms I, II and III, corresponding to positions at which the fractional light intensities were ·046, ·043, ·0073, respectively. Forms IV and V are from dry and wet positions respectively, corresponding to the same fractional light intensity, namely ·0041.

The thallus of Form I was broadly dichotomising (Fig. 1, *1*), and shewed the following typical[2] structures (Fig. 1, *2*). (1) Air chambers with elliptical pores, and flasked-shaped assimilating filaments. (2) Ventral scales. (3) The two kinds of rhizoid—tuberculated and smooth—the tuberculated rhizoids produced in bundles in the axils of ventral scales, and running horizontally, approximating to the under surface of the thallus, the smooth-walled rhizoids growing vertically downwards. (4) Mucilage sacs in the midrib and in the lateral wings of the thallus. (5) Two or three rows of assimilating tissue underlying the epidermis. (6) Ventral tissue consisting of large colourless storage cells; in the ventral tissue of the wings two or three rows of these cells containing starch, and having their walls thickened by anastomosing bands of cellulose, the unthickened portions remaining as slits; in the ventral tissue of the midrib several layers of smaller storage cells. (7) Mycorrhiza in the colourless storage tissues underlying the assimilating tissue, especially in the tissue of the midrib. Typical thalli of Forms II and III shewed the following variations.

---

[1] Cf. Wiesner's method for the "Lichtgenuss" of plants: J. Wiesner, "Der Lichtgenuss der Pflanzen," 1907, p. 4.

[2] F. Cavers. "On the Structure and Biology of *Fegatella conica*." Ann. Bot., Vol. 18, 1904.

(1) A decrease in the size of the thallus, accompanied by a decrease in the average number of air chambers per unit of surface area, and in the average size of the pore of the air chamber. These facts are shewn in the following table :—

TYPE OF THALLUS.		I.	II.	III.
Fractional light intensities		·046	·043	·0073
Size of typical thallus ...	Length Breadth	4·5 cm. 1 cm.	3 cm. ·5 cm.	3 cm. ·5 cm.
Average number of air chambers per sq. cm.		57	35	32
Size of air chamber pore	Average length of major axis of ellipse ..	·072 mm.	·047 mm.	·041 mm.
	Average length of minor axis of ellipse ...	·041 mm.	·029 mm.	·027 mm.

(2) A broadening of the upper narrow portion or neck of the assimilating filaments (Fig. 1, *3-5*).

(3) The presence of chloroplasts in the neck of the assimilating filaments of Form III contrasted with their limitation to the swollen basal portion of the filaments of Forms I and II.

(4) The presence of chloroplasts in the epidermal cells of Forms II and III (ranged along the lower wall parallel to the surface of the thallus), contrasted with the absence of chloroplasts in the epidermal cells of Form I.

The large majority of thalli of Form IV and all the thalli of Form V shewed marked reduction in form and structure. The difference in degree of moisture in the respective positions was due to a continuous stream of slowly dripping water in which the thalli of Form V were growing.

In both forms the thalli were considerably narrower and thinner than in Forms I, II and III. A typical thallus of Form V however was narrower and more elongated than one of Form IV (Fig. 1, *6*, *7*). In the majority of thalli of Form IV and all of the thalli of

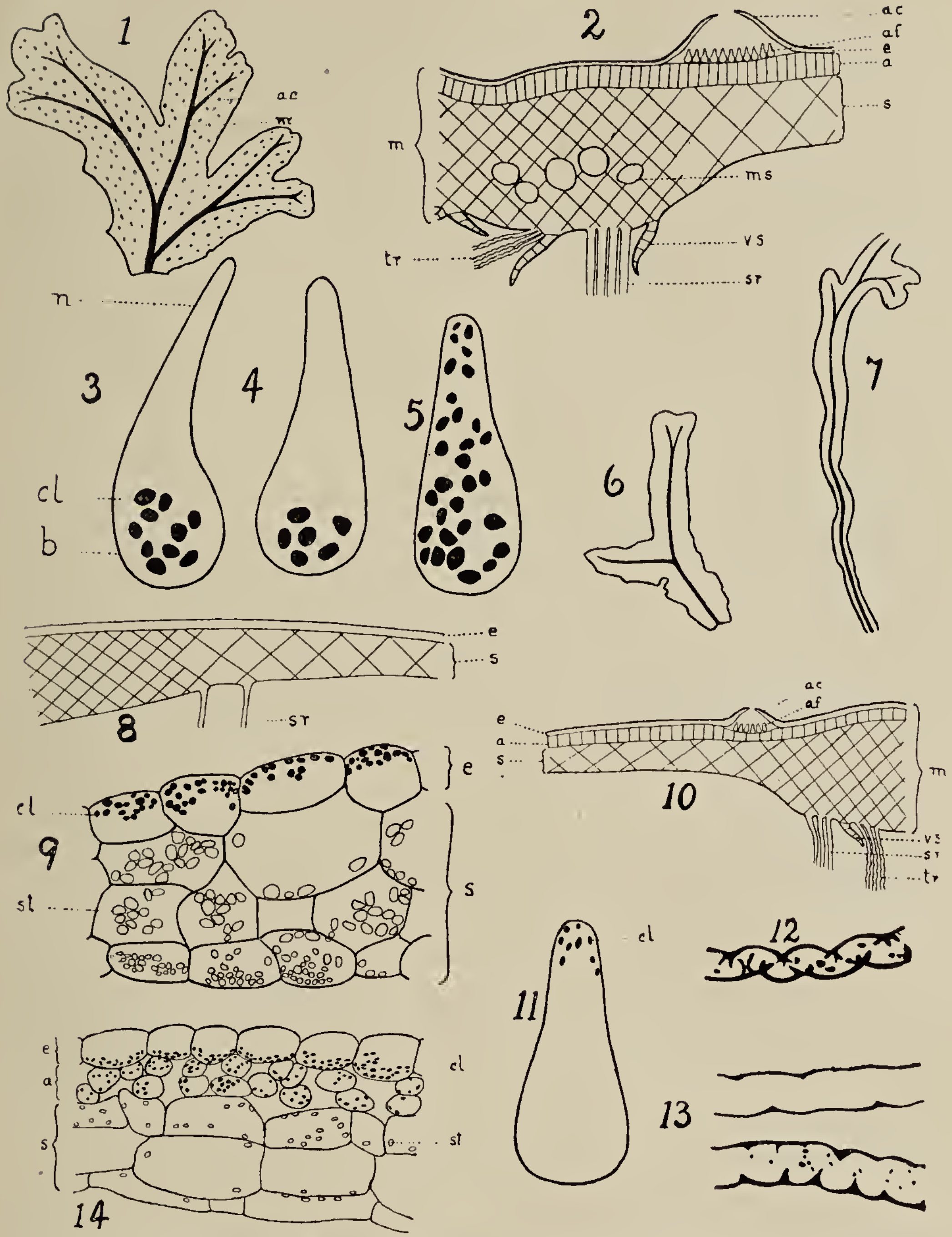


FIG. 1. *Fegatella conica.* 1, diagram showing typical thallus of Form I (see Text), nat. size; 2, transverse section (diagrammatic) of thallus of Form I, × 20; 3, 4, 5, assimilating filaments of Forms I, II and III, respectively, × 350; 6, 7, diagrams showing typical thalli of Forms IV and V respectively, nat. size; 8, transverse section (diagrammatic) of thallus without air chambers, × 50; 9, part of this thallus, × 80; 10, transverse section (diagrammatic) of thallus of transitional form, × 50; 11, assimilating filament of transitional form, × 350; 12, tuberculate rhizoids of Form I, × 350; 13, tuberculate rhizoids of transitional form showing reduction in tuberculation, × 350; 14, part of thallus of transitional form, × 80.

Lettering: *a.*, assimilating tissue; *a. c.*, air chamber; *a. f.*, assimilating filament; *b.*, basal portion of assimilating filament; *cl.*, chloroplast; *e.*, epidermis; *m.*, midrib; *m.s.*, mucilage sac; *n.*, neck of assimilating filament; *s.*, storage tissue; *s.r.*, smooth rhizoids; *st.*, starch grain; *t.r.*, tuberculated rhizoid; *v.s.*, ventral scale.

Form V, there were no air chambers, ventral scales or tuberculated rhizoids. A few smooth-walled rhizoids were produced on either side of the midrib, the latter being somewhat less pronounced than in Forms I, II and III. The structure of the individual thallus was uniform throughout, shewing complete absence of assimilating tissue and mucilage sacs (Fig. 1, *8*). The epidermis contained numerous chloroplasts which were ranged along the upper walls of the cells (Fig. 1, *9*). The rest of the thallus consisted of large colourless storage cells containing starch grains. The walls of the storage cells were not thickened by anastomosing bands of cellulose as in Forms I, II and III.

There has been no previous record of the occurrence in nature of forms of *Fegatella conica* without air chambers, although, in the light of recent observations on *Dumortiera*,[1] one is led to suspect that, given the necessary conditions, such a form would arise. The only conclusive evidence that the thalli of Forms IV and V belong to *Fegatella conica* would be one of culture, but it is very improbable that they should belong to any other member of the Marchantiales —firstly, because *Fegatella conica* was the only liverwort growing anywhere around, and secondly, because of the existence of the transitional form described below. Maheu[2] describes the general appearance of *Fegatella* plants growing in the most feebly illuminated deeper portions of ditches, stream-sides, and holes; in extreme cases there was practically no rosette formation, the individual plants being greatly elongated (as long as 25 to 30 cm.), very slightly branched (usually only once), very narrow (less than 5 mm. broad), extremely thin and tinged only slightly green so as to be quite transparent, while the dome-like roofs of the air-chambers were absent and the upper surface of the thallus thus quite flat.

It has already been shewn how a reduction in the fractional light intensity has been accompanied by a reduction in the size of the thallus, and in the number and size of the air chambers (see Table). Now among the thalli of Form IV were found a few pieces which possessed air chambers, but which shewed a nearer approximation to thalli of Forms IV and V than did thalli of Form III.

Compared with thalli of Form III, the air chambers of this transitional form shewed a reduction in number, namely 28 per sq. cm. as compared with 32 per sq. cm. in Form III. The average size of the air chamber pore, however, was the same as in Form III. The ventral scales were smaller and fewer than in Form III, two rows only being produced, one down either side of the midrib. Tuberculated rhizoids were present in bundles in the axils of the ventral scales, but were growing vertically downwards, not horizontally, approximating to the lower surface of the thallus as in the normal form (Fig. 1, *10*). The assimilating filaments of the air chambers were flask-shaped with broad necks, approximating in form those found in Form III. The chloroplasts however, had all migrated to the neck, especially the tip (Fig. 1, *11*). The ingrowths of the cellulose walls of the tuberculated rhizoids were less marked than in Forms I, II and III (Fig. 1, *12*, *13*), and thus, both in position and structure, shewed an approximation to the smooth-walled type of rhizoid. Chloroplasts were present in the epidermis, and were ranged parallel to the surface along the lower walls. There were two layers of loosely compacted assimilating cells, containing chloroplasts ranged more or less parallel to the surface of the thallus. The ventral tissue consisted of large colourless storage cells with unthickened walls. There was a complete absence of mucilage sacs (Fig. 1, *14*).

---

[1] W. C. Coker. "Selected Notes. II. Liverworts." Bot. Gazette, Vol. 36, 1903, p. 225.

[2] J. Maheu. "Monographie des principales déformations des Muscinées cavernicoles." Compt. rend. Congr. Soc. sav., Paris, 1907, p. 343.

The only two members of the Marchantiales which have been described as devoid of air chambers and assimilating tissue are *Monoclea* and *Dumortiera*. *Monoclea* has never been found with air chambers. The habitual absence of air chambers and ventral scales, together with the feeble development of the invaginations of the cellulose walls in the tuberculated rhizoids has been correlated with the hygrophilous habitat of the plant.[1] *Dumortiera*, however, has been found to produce well-developed air chambers under dry conditions. Coker[2] found that plants of *D. hirsuta* growing on a porous sandy soil produced air chambers, whilst the same plants grown in dripping water shewed no trace of air chambers. In this case, therefore, the absence of air chambers is to be correlated with the hygrophilous habitat. Coker concluded that the simple form of *Dumortiera* is secondary, and the loss of air chambers is no doubt correlated with the semi-aquatic mode of life of this genus.

Partial reduction of the air chambers has been noted in several members of the Marchantiales. Wheldon,[3] speaking of the group as a whole, says that under more aquatic conditions the air chambers

[1] F. Cavers. "The Inter-Relationships of the Bryophyta. Marchantiales." New Phytologist, Vol. 9, 1910, p. 108.

[2] W. C. Coker. *Loc. cit.*

[3] J. A. Wheldon. "Social Groups in the Bryophyta." Lancashire Naturalist, '11.

are much reduced, and the pores fewer. Cavers[1] noted that in submerged plants of *Marchantia* the air chambers shew great reduction. Reduction in number and size of the air chambers of *Fegatella conica* has been correlated with both factors of light and moisture. Cavers[2] says, in connexion with the asexual reproduction of this genus, "when cultures were made in darkness" (*i.e.*, cultures of cut pieces of thalli on damp soil) "new shoots were formed quite as freely as in the light, but they were long and narrow, and *did not grow into normal plants with typical air chambers and scales.* On being brought to light they gave rise to normal plants, otherwise they remained abortive after attaining a length of 2 to 3 cm." Bolleter[3] noticed that when thalli of *Fegatella conica* were found growing on very damp soil, the air chambers were reduced in number and size. He does not mention total disappearance, however.

In the *Fegatella* found in the cavity already referred to in this paper it is obvious that a decrease in light has been an important factor in causing the reduction in number and size of the air chamber (see Table). The factor of moisture, however, has probably played an important part in the final disappearance of the air chambers. The similarity in structure of Forms IV and V and the possession by the former of distinctly aquatic modifications, namely, the absence of ventral scales, tuberculated rhizoids, and mucilage sacs and canals, lead one to suspect that the simplicity of structure was brought about in the first place by conditions of moisture. Cavers[4] and later Bolleter[5] concluded that the function of the filaments of the air chambers is that of transpiration, the former having proved experimentally that evaporation of water is localised in these pointed cells. It is quite conceivable, therefore, that an increased water supply would be an important factor in the elimination of the air chambers. These authors agree in stating that the chloroplasts are confined to the basal portions of the filaments. In Form III and in the transitional form here described, however, chloroplasts were distinctly present in the neck. In the transitional form they were even limited to the neck. This appears to point to an assimilatory as well as a transpiratory function, the

[1] F. Cavers. NEW PHYTOLOGIST, Vol. 9, 1910, p. 108; Ann. Bot., Vol. 18, 1904, p. 87.

[2] F. Cavers. Ann. Bot., Vol. 18, 1904, p. 97. (The italics are mine).

[3] E. Bolleter. "*Fegatella conica.*" Beihefte zum Bot. Centralbl., Band 18, 1905.

[4] F. Cavers. Ann. Bot., Vol. 18, 1904, p. 91.

[5] E. Bolleter. *Loc. cit.*

chloroplasts in the shade forms taking up this position so as to gain maximum intensity of light. It is quite probable, therefore, that decrease in light aided in the disappearance of the assimilating filaments, and therefore of the air chambers, just as decrease in light has been accompanied by decrease in assimilating tissue, whose function has been taken over by the enlarged epidermal cells.

As regards the variation in form of the thallus found in the decreasing light intensities, it is interesting to compare Miss Greenwood's results with *Pellia epiphylla*.[1] She found that those thalli growing in shaded places take on a narrow slender shape, and those having a greater exposed surface fork and fork again and broaden out horizontally.

Further, Cavers[2] mentions that thalli of *Fegatella* are elongated and narrowed in darkness. Bolleter[3] however correlates elongation and narrowing of thalli of *Fegatella* with conditions of moisture. It is quite probable that both darkness and moisture have been instrumental in producing this variation of form.

SUMMARY.

Thalli of *Fegatella conica* without air chambers were found in a hole in a bank. The absence of air chambers is concluded to be due to the combined effect of darkness and moisture. For in thalli growing in increased intensities of light there is a gradual decrease in the number of air chambers per unit of surface area, and in the size of those air chambers. The final disappearance, however, seems to be dependent on the factor of moisture, for only in those forms shewing marked adaptations to a moist habitat were the air chambers totally lacking. This case adds to the number of Marchantiales already known as occurring without air chambers.

The above piece of work was carried out in the Botanical Laboratory of Westfield College, under the supervision of Dr. E. M. Delf, to whom I wish to express my thanks.

WESTFIELD COLLEGE,
HAMPSTEAD, LONDON.

---

[1] Helen H. Greenwood. "Some stages in the development of *Pellia epiphylla*." The Bryologist, Vol. 14, 1911.

[2] F. Cavers. Ann. Bot., Vol. 18, 1904, p. 97.

[3] F. Bolleter. *Loc. cit.*

A NEW BOOK ON PALÆOBOTANY.

Pelourde, F. "Paléontologie végétale. Vol. I. Cryptogames cellulaires et cryptogames vasculaires." *Encyclopédie scientifique Doin*, Paris, 1913. Price 5 francs.

THE task of writing an encyclopædic treatise on Palæobotany is by no means an easy one. The ground to be covered is so large, from Bacteria to flowering plants and from the far distant Palæozoic epoch almost to the present day, that the selection of material must be very difficult. At the same time the interest of fossil types lies so frequently in the details of their structure that the limitations of space to describe it must be all the more heavily felt. In the present volume, however, Dr. Pelourde has succeeded in giving an excellent account of the fossil cryptogams in the short space of about 320 small pages, of which about 300 are devoted to the Pteridophyta. As a short summary of our knowledge of the past history of these plants, it is a work of conspicuous merit, for though it may not contain sufficiently detailed descriptions to serve as a text-book for the more advanced botanical student, it contains much interesting matter and has the great merit of being easy to read. The text is accompanied by a fairly full list of references to the more important literature. The plants which are known only from impressions receive proper attention, in addition to those whose structure has been investigated, and thus a fairly clear picture of the fossil types is obtained. Most of the present volume is concerned with Palæozoic plants, but the Mesozoic forms are also frequently mentioned and occasionally figured; nevertheless some of the Mesozoic and Tertiary genera, which throw light on the ancestry of some of the modern ferns and of *Equisetum*, are rather neglected.

Towards the somewhat complex nomenclature of fossil plants, the author adopts a very conservative attitude, the well-known Sphenophyllacean cones are spoken of as *Bowmanites Dawsoni*, though the figure is labelled *Sphenophyllum Dawsoni*, and Scott's species is spoken of as *Sphenophyllum fertile*. Among the ferns we notice that the generic name of *Zygopteris* is used in the older sense to include all forms with an H-shaped petiolar xylem, and the newer terms *Ankyropteris* and *Etapteris* are not employed.

The first section gives a short summary of the fossil Thallophyta and Bryophyta. This is followed by an account of the Equisetales which is very clearly written; the different types of stems and of cones are briefly described, and the account completed by reference to the form and structure of the roots and the leaves. While good figures are given of the other types of cone, the figure of *Calamostachys* is very diagrammatic, and though *C. Binneyana* is described as the typical form, the figure does not give any indication of the structure or vascular supply of the sporangiophores and shows bundles which alternate at the level of the bracts. The structure of the vascular system of this cone is of great importance not only in relating it to the other Equisetalean types, but also in the discussion of its relations to the Sphenophyllales and of the morphology of the sporangiophore, and under these circumstances a new and more correct figure might have been given. The account of the Sphenophyllales is perhaps the best section in the book, and is probably the best brief summary of this group which has yet been written. The interesting Devonian form *Pseudobornia* is accorded a figure and a brief description and is regarded as representing a distinct group—the Pseudoborniales. Dr. Pelourde considers the Sphenophyllales as constituting a synthetic group more or less closely connected to the Pseudoborniales, Equisetales, Psilotales and Lycopodiales.

The sections devoted to the Lycopodiales contain an immense amount of summarised information with a great many references to the extensive literature on the subject. The author is certainly to be congratulated on the way in which he has managed to give a survey of so much in such a small space. Sometimes we are inclined to wonder what sort of impression this very condensed section would produce on the mind of one who was reading about these plants for the first time.

No doubt the fossil ferns present greater difficulties than any other group in a book of this type, and the author does not seem to have been quite so successful in his treatment of them. This is due almost solely to the manner in which the material has been arranged. Under the heading Filicales we have a list of the principal classes of modern ferns, followed by a description of the various forms of fossil fern-like fronds which are known for the most part from impressions. The next chapter is devoted to a short summary of some of the different types of fern sporangia found in a fossil state, including both impressions and petrified forms. Some of the sporangia described are only known as isolated structures, while others can be connected with the stems of the plants which bore them with some degree of certainty, as in the case of *Stauropteris oldhami*. The last section is devoted to the description of the anatomical structure of the various forms, where this is known, and though in most cases the vegetative parts only are described, the sporangia are sometimes mentioned. Probably the author had good reasons for dividing up his material in this way, but he undoubtedly lays himself open to a good deal of criticism, and the plan usually followed of describing consecutively the fronds, sporangia and structural features of each genus or group seems greatly preferable. Under the system employed here it is necessary to consult the index in order to get an idea of the complete plant of such a form as *Botryopteris* or *Stauropteris*, while the chapter on the fructification is robbed of much of its interest, It would certainly seem out of date to group together the Palæozoic fern-like fronds under the heading of the Filicales, for as the author notes at the outset many of these fronds were pteridospermic. The question as to whether the Pteridosperms or the Filices predominated in the Coal Measure period is an old one, but there can be no doubt that many of the fern-like Carboniferous fronds bore seeds and if no attempt is to be made to separate the known pteridosperm fronds from the known filicinean fronds the composite group should be placed under a separate heading rather than among the Filicales. And it should be pointed out more clearly that the system of classification of these fronds is a purely artificial one, since under the Eu-Pecopterideae are included *Pecopteris* the majority of whose fronds are said to belong to the Marattialian alliance though *P. Pluckneti* is a pteridosperm, and *Thinnfeldia*, whose affinities, though uncertain, are almost certainly not filicinean.

In the section devoted to the anatomical structure of the fern groups, a good account appears of the *Psaronius* types of stem and emphasis is given to the view that the variations observed in the structure of the leaf-scars and foliar traces of *Caulopteris* and *Stipitopteris* correspond to differences in level and have little systematic importance. Dr. Pelourde has adopted the term Botryopterideae (Botryoptéridées) for the group including the interesting Palæozoic genera of the Botryopteridean and Zygopteridean type. The rather wider term Coenopterideae, introduced by Professor Seward to include this group with its varied forms, does not seem to have as yet gained general acceptance, partly because some authors seem to consider that a generalised type must necessarily exhibit a simple form of structure and regard the group as specialised rather than generalised, and also because they seem to leave out of consideration the sporangial structure in these plants. The more important types in this group are briefly described, and in summarising their relations the author adopts the views of Kidston and Gwynne-Vaughan with reference to the inter-relationships of the Zygopteroid forms. The majority of the forms are separated into three lines, one headed by *Clepsydropis*, the other two leading through *Dineuron* to a hypothetical common ancestor allied with the primitive Osmundaceae.

In summarising the ferns it is further pointed out that the Palæozoic sporangia show transitions between the Osmundaceae and the Marattiaceae through *Discopteris* and *Diplolabis* and between the Osmundaceae and Schizæaceae through *Kidstonia* and *Seftenbergia*.

At the end of the book is a short bibliography in which we notice that the papers by Professor F. E. Wiess of Manchester are mingled with those of the late Prof. C. E. Wiess of Berlin without distinction.

In spite of the criticisms made above the present work is undoubtedly a very useful little volume, and gives a good survey of the fossil pteridophytes in a small compass. At the very modest price of five francs it should find its way into the libraries of many English botanists, and we look forward to the appearance of the two remaining volumes.

THE
NEW PHYTOLOGIST.

Vol. XIII, No. 8. October, 1914.
[Published October 26th, 1914.]

THE ANTAGONISM BETWEEN IONS IN THE ABSORPTION OF SALTS BY PLANTS.

By Walter Stiles and Ingvar Jörgensen.

Introduction.

IN this paper we propose to deal with the antagonism that exists between salts, or more properly between ions, in their absorption in water solutions by plants.

That the presence of certain salts in the nutrient solution of plants influences the specific effect produced by others has now been recognised by agriculturists and agricultural botanists for many years, and in consequence many experiments have been performed with the object of determining more definitely the nature of such mutual influence of salts. Thus a large literature dealing with such experiments is to be found in journals devoted to the recording of agricultural experiments. Yet the methods in common use among agriculturists have not resulted in much definite information.

Even now the laws governing absorption of salts by plants are little understood, but during the last few years the application of the methods of plant physiology has brought several fresh ways of attack. The work which has resulted along several different lines has produced more hopeful results, and although our knowledge of these questions is still in its infancy, yet several quite definite facts are becoming clear. Perhaps the most interesting of these, the one with which we intend to deal in this paper, is that of the mutual hindrance to their absorption produced by ions with a charge of the same sign—the phenomenon now generally known as antagonistic ion action.

EARLIER WORK AND WORK NOT DEALING DIRECTLY WITH ANTAGONISM.

The first indications in plant physiology of the existence of the phenomena we are considering, were very naturally observed with the advent of the method of water-culture, where the constitution of the nutrient solution is under the control of the investigator. Sachs (34, 35) in his classical researches with this method observed that plants grew best when a certain balance was maintained between the various constituents of the nutrient solution; a result which becomes in some part explicable now on the theory of antagonism. Some years later Boehm (3) showed that the toxicity produced by certain salts when present alone in solution—an effect which had previously been noted by Wolf (40) in the case of weak solutions of potassium, sodium and ammonium salts, and of very weak solutions of magnesium salts—could be lessened or eliminated by the addition to the solution of small quantities of calcium salts, which Wolf had shown were much less toxic in pure solution than salts of magnesium or of the alkali metals.

In 1898 Benecke (1) also showed that the toxic action of potassium salts was eliminated in the presence of calcium salts.

One of the results of the water-culture method has been the emphasising of Sachs original observation of the necessity for a balance between the various constituents of the nutrient solution, and special attention has been directed towards the optimum ratio of calcium and magnesium in nutrient solutions. Some workers at any rate seem to have obtained definite evidence of a calcium-magnesium ratio best suitable for plant growth. But the results of different workers show little consistency in details, and here it will be sufficient to refer to the work of Loew (15), Loew and May (19), Kearney and Cameron (12), Gile (9), True and Bartlett (38) and Tottingham (37), who have all produced evidence of the balance required between different nutritive substances, and in particular between calcium and magnesium, for the production of an optimum absorption of salts, or growth.

Before ideas on antagonism had taken a definite form Loew (15, 16) elaborated a theory to account for the toxic properties of magnesium when calcium was not present in sufficient quantity. He supposed calcium is a necessary constituent of the chlorophyll-bodies and nucleus, and when magnesium is present in great excess this takes the place in those bodies that should be occupied by calcium. This causes a structural disturbance of account of which the protein substances cease to be active and death ensues. It will be observed that this theory will only explain the need for a balance between calcium and magnesium; it is not a general theory of antagonism. In the case of calcium and magnesium the seat of the antagonistic action on this theory is inside the cell in the nucleus and plastids; in this respect, as we shall see later, Loew's theory differs fundamentally from the opinions arrived at by some more recent workers.

WORK DEALING DIRECTLY WITH ANTAGONISM.

The modern conception of antagonism is due to Loeb who commenced publishing on this subject in 1901; a general account of his work appears in his "Dynamics of Living Matter" (14). He worked on the development of *Fundulus* eggs in various solutions. He found that these eggs are unable to form an embryo if put immediately after fertilization into a solution of pure NaCl of the same concentration as that of this salt in sea-water. This toxicity is reduced if a small definite quantity of the salt of a bivalent metal is added to the NaCl solution. The salt of any bivalent metal is able to produce this effect except those of very poisonous metals such as mercury; even such poisonous salts as those of lead are able to produce this result. That this effect is due to the kation was shown by using different salts of the same metals. Trivalent kations were also capable of rendering the toxicity of salts of univalent metals less harmful; but a tetravalent kation, thorium, was found to have only a slight depoisoning effect. The reverse is also true, for monovalent ions were found capable of reducing the toxicity of salts of zinc. A slight antagonism was also observed between two divalent kations, such as Sr and Mg.

The relative quantity of the depoisoning ion that has to be added varies with the concentration of the toxic solution. Thus with *Fundulus* a concentration of $\frac{M}{4}$ NaCl is harmless; with a concentration of $\frac{5}{8}$ m NaCl one bivalent ion is required to render 1000 Na ions harmless. Between these two concentrations of NaCl the relative quality of bivalent ion required is less, while it is impossible to render harmless a solution of NaCl above a certain concentration.

It is interesting that these antagonistic effects only hold for the eggs and not for the larvæ of *Fundulus*. Loeb, therefore, concludes that the antagonistic effects only appear so long as the fish is surrounded by the egg membrane, and that they are actually due to the two kinds of ions mutually hindering one another's diffusion into the egg.

The work of Loeb on animals has been continued and developed by Osterhout with much ingenuity with regard to plants. In order to determine the relative toxicity of the various solutions used he has made use of four different methods, which will be described in connection with the experiments in which they were used.

Osterhout's first experiments (23) were made with marine plants and his observations on these were afterwards extended to freshwater and land plants. Marine plants he found can be divided into two groups: those which are quickly killed when placed in distilled water and those which can live a long time in distilled water. Plants of the latter group are killed much quicker when placed in a pure sodium chloride solution isotonic with sea water than when kept in distilled water. The poisonous effect of the sodium chloride largely disappears if a little calcium chloride is added. In a mixture of 10cc $CaCl_2 \frac{3m}{8}$ + 1000cc $NaCl \frac{3m}{8}$ the plants live nearly as long as in distilled water. If some potassium chloride is added to the mixture they live longer than in distilled water, while with further additions of $MgCl_2$ and $MgSO_4$ they live practically as long as in sea water.

Potassium or magnesium chloride added singly inhibit the toxicity of sodium chloride a little, but are not nearly so effective as calcium chloride. The mixture $NaCl + KCl + CaCl_2$ is better than $NaCl + MgCl_2 + CaCl_2$, which is itself superior to the mixture $NaCl + MgCl_2 + KCl$.

As Osterhout justly observes the effects must be due to the metal ions, as practically the same amount of the same anion is always present. Moreover the effect cannot be merely a starvation phenomenon as distilled water alone is less harmful than sodium chloride alone or the mixture of sodium and calcium chlorides.

Similar results were obtained with the plants which were quickly killed in distilled water, except in their behaviour to the latter medium.

In his experiments with terrestrial and fresh water plants (24) a variety of genera were used: *Vaucheria*, *Spirogyra* and other algæ, *Lunularia* (gemmæ), *Equisetum* (spores and prothallia) and Wheat seedlings among others. A similar result was obtained in these cases although diluter solutions were used.

From these experiments Osterhout derives the conception of physiologically balanced solutions. He supposes that a number of toxic substances present together in a solution are rendered non-toxic if they are present in a certain ratio. Such a solution is a physiologically balanced one.

Osterhout also points out that a nutrient solution may be used in which the dissolved substances are present in such dilution that none of the components would exert any toxic action if the others were removed. It is obvious that in this case the question of a physiological balance does not enter; only when the concentration is increased beyond a certain strength will the solution become toxic to plants and a physiological balance be required between the various solutes if the solution is to do no harm.

In a third series of experiments the antagonism between potassium and magnesium alone is dealt with (26). Species from most of the great classes of the plant kingdom were tried and it was shown that a solution containing both potassium and magnesium chloride in a definite ratio is less toxic than pure solutions of either salt in the same molar concentration.

It was also shown that in the case of the nitrates and sulphates the addition of the potassium salt to the corresponding magnesium salt reduces the toxicity of the latter.

Osterhout thus disposes of the theory of Loew and Aso (18) that the antagonism is due to the formation of a double salt of potassium and magnesium chloride, for the nitrates do not form double salts. Moreover in the case of chlorides the salt would dissociate into its constituent ions, and the result in solution would be much the same.

In these experiments it will be observed that Osterhout generally determines the relative toxicity by measuring the length of life of the structure under consideration; the death point was easily noted by observations of the colour reactions and microscopic appearance of the cells.

In some cases, as for instance in those experiments on *Equisetum* prothallia and Wheat seedlings, he uses the amount of growth as a criterion of relative toxicity. This method is elaborated in a further paper (27) on the protective action of sodium on plants in which the mutual action between sodium and potassium, sodium and ammonium, sodium and magnesium, and sodium and calcium is investigated by means of measuring the growth in length of roots of Wheat seedlings and other plants. He worked principally with the chlorides but obtained analogous results with nitrates. In each case he found the toxicity of a mixture of the two salts was less than that of either salt singly, the concentration (0·12M) being constant throughout the experiments. In each case there is a definite ratio of the two constituents of the solution which gives a maximum growth. Above and below this ratio there is a falling off which is greater the further removed the ratio is from the optimum. Similar results were obtained in soil experiments.

Osterhout concludes from these researches that sodium is not useless but has a protective effect on plants, a question to which he returns in a later paper (30). He conceives "normal life as possible only when the necessary salts combine with the colloids of the living substance in a definite ratio." This ratio it is supposed will be dependent upon the composition of the solution outside the plant according to the law of mass-action. He emphasises the fact that antagonism does not depend merely upon an action between the salts themselves, but upon their action on the living substance.

In his next experiments Osterhout demonstrates antagonism by means of plasmolysis (28). Having previously shown (25) that the contraction produced by a salt solution may not be true plasmolysis at all but a contraction resembling it, due to the toxic effect of the salt itself entering, the necessity of care in distinguishing true plasmolysis is emphasised. He finds that

Spirogyra plasmolysed in ·2M $CaCl_2$ but not in ·195M $CaCl_2$
" " " ·38M NaCl " " " ·375M NaCl.

It is, however, promptly and very markedly plasmolysed in a solution of 100cc ·375M NaCl + 100cc ·195M $CaCl_2$ showing, therefore, the non-entrance into the cell-sap of the salt in the case of a mixture of these chlorides, while in the case of single salts of the same concentration the salt diffuses through the plasma-membrane as well as the water, and so no plasmolysis is produced.

The most ingenious of Osterhout's methods for demonstrating antagonism is undoubtedly that in which he uses the difference in electrical resistance of living and dead tissue to determine the rate at which single salts or mixtures of salts kill *Laminaria* (29). Discs of the flattened laminæ of this alga were cut out by means of a cork-borer, and from 100 to 200 of them packed closely together to form a compact cylinder of tissue. At each end of the cylinder was a platinum electrode. The resistance of the whole cylinder of discs was then measured by means of Kohlrausch's method. The resistance of the cylinder of living tissue in sea water was found to be 1110 ohms, when dead in a solution of the same electrical conductivity as sea water, the resistance was only 320 ohms. The extra resistance can only be due to the resistance to the passage of the ions by the plasma-membranes of the living cells, this extra resistance disappearing when the cells are dead and the membranes become completely permeable.

By this method it was shown that calcium chloride was much less toxic than sodium chloride, but that a mixture of the two in the proportion of 1000cc M.NaCl to 15ccs. M.$CaCl_2$ diluted till its conductivity equalled that of sea water retained its original resistance for 24 hours. This can only be ascribed to the cell membranes retaining their property of impermeability to the two combined ions, so that here we have a demonstration of antagonism by a most original and striking method.

The earlier observations of Osterhout have been extended by Hansteen (10), who in a somewhat lengthy paper gives the results of experiments on the antagonism between potassium and other metallic ions. He worked with a wide range of concentrations, the solutions being as a rule much diluter than those of Osterhout. He used nitrates as a rule, but occasionally other salts.

His method consisted in growing seedlings of a Norwegian variety of Wheat for 14 days. His first experiments were made with solutions of single salts to determine the specific effect of each metallic ion on root development. Later he used mixtures of potassium nitrate and the antagonising salt. In any series the concentration of any solution was constant, but the ratio of K to the antagonistic kation varied. The cultures were done in duplicate.

The toxicity was determined by means of measuring the dry weight of the roots produced. Observations were also made on the appearance of the roots.

As a result of these experiments Hansteen records a definite antagonism between potassium and calcium, and between potassium and magnesium (though it is not very great); between potassium and sodium he found a little, though scarcely noticeable, antagonism.

His results differ in many details from those of Osterhout's. Thus in the case of potassium and magnesium he found the optimum ratio was given by the mixture $100\ \frac{M}{100}\ KNO_3 + 4{\cdot}0625\ \frac{M}{100}$ $Mg(NO_3)_2$, whereas Osterhout finds the best mixture with chlorides to be $100\ 0{\cdot}0375M\ KCl + 25\ 0{\cdot}0375M\ MgCl_2$, a very different ratio; but of course the concentrations and the anions are different in the experiments of the two observers.

Again, Osterhout found a very well marked antagonism between potassium and sodium. Here, again, Osterhout worked with higher concentrations.

Hansteen criticises this result of Osterhout's in that it may have been due to his keeping the seeds in the solution. The seeds are supposed to have excreted substances which eliminated the toxic effect. This criticism seems, however, to be scarcely valid, as one would expect the excreted substance to paralyse the effect in all the solutions used by Osterhout.

Osterhout is further criticised in that he says antagonism does not enter into dilute solutions, while Hansteen shows there is an antagonism even in solutions of as low a concentration as $\frac{M}{800}$.

But Hansteen's whole work is open to the very serious criticism that it is based on observations of the appearance, and measurements of the dry weights, of roots of water cultures grown in duplicate. Anyone who has conducted research work involving the use of water cultures will realise how unsafe it is to generalise on such cultures done only in duplicate owing to the great variability of such plants even when growing under exactly similar conditions. So that while it seems safe to accept Hansteen's general result of the antagonism between the nitrates he used, yet it would appear more satisfactory to delay the acceptance of the actual optimum ratios he records until they have been confirmed hy a more numerous series of controls or by some other method.

In order to arrive at the reason for the depoisoning effect of calcium on magnesium or potassium, Hansteen performed some experiments in "double cultures." In these, seedlings of Wheat or Oat were grown with some side roots in a tube containing a pure magnesium or potassium nitrate solution and with other side roots of the same seedling in a pure calcium nitrate solution or a mixture of calcium nitrate with magnesium or potassium nitrate. In all such cultures the roots growing in the tube containing calcium nitrate were healthy while those in pure potassium or magnesium nitrate perished. The same result was obtained when the plumule was in gypsum. In all such experiments it was shewn by microchemical examination that plenty of calcium had diffused into those roots immersed in magnesium or potassium nitrate. From this result Hansteen concludes that the antagonism between calcium and magnesium or potassium is a surface effect, and not due to chemical action inside the cell.

A modification of this method was also employed in which the root grew in bent tubes with different parts of the same root in different solutions, and the same conclusion was reached in these experiments also.

By determinations of the $\frac{\mathrm{Ca}}{\mathrm{Mg}}$ ratio of seeds he shows that the relative quantity of calcium in the seedling is independent of its behaviour in a pure magnesium salt solution, thus affording a further piece of evidence in favour of the view that the value of calcium lies in its effect at the surface between the absorbing membrane and the external solution, and is not due to chemical action inside the cell. With the further conclusions of this worker we intend dealing in the last section of this paper.

The work of Osterhout and Hansteen has been supplemented by McCool (20) so as to comprise an investigation of the mutual antagonism of a larger number of kations. He experimented upon Wheat and Canada Field Peas. Seeds were germinated between damp filter papers and the seedlings so obtained were transferred to the culture jars containing the solution. The jars were not very large to judge from the photographs of the cultures, and several seedlings grew in one culture jar. The cultures appear to have been done singly, not even in duplicate, and the results given appear to be based on such single cultures. The plants were allowed to grow for from 21 to 30 days, after which the length and the fresh weight of shoots and roots were taken. By this method McCool has shown antagonism between calcium and a large number of other kations: magnesium, potassium, sodium, ammonium, barium and strontium. Magnesium and potassium were also found to exert an antitoxic effect upon the very poisonous barium, while magnesium, potassium and sodium were each found capable of reducing the toxicity of strontium. Mutual antagonism was also recorded between sodium and both potassium and ammonium.

A few quantitative relations are also recorded, but it is obvious that the observations are spread over too wide a field to enable many exact quantitative measurements to be made. As the writer himself says, much remains to be done in this direction.

In a further series of experiments the same worker has investigated the antitoxic action of various kations in regard to manganese. He finds the poisonous effect of manganese is counteracted by calcium, potassium, sodium and magnesium ions.

A most interesting advance in our knowledge of antagonism has been recently made by Szücs (35). Regarding antagonism as due to the mutual hindrance to one another's entrance of two similarly charged ions he investigates the antagonism between copper and aluminium.[1]

For reasons with which we need not deal here, Szücs did not determine the death points of the plants upon which he experimented, but the time taken for the plants to absorb enough of the toxic substances to kill. In order to do this he made use of the geotropic reaction of the hypocotyl and seedling root as indicator of the toxic action. The species used was *Curcubita Pepo.* After varying times of immersion in the solution the seedlings were removed and placed with their axes in a horizontal position under a bell jar in moist air. After 24 hours the number of plants which exhibited the geotropic reaction was noted. A longer period of immersion resulted in fewer seedlings responding to the reaction: the time of immersion required to kill was taken as the time required in order that 70% of the seedlings should no longer respond to the reaction.

This method is open to the objection that owing to the differences exhibited in individual plants a very large number of seedlings is required in order to get a reliable result in each experiment. This difficulty Szücs' own numbers clearly show; nevertheless the method is decidedly ingenious.

Szücs shows that aluminium chloride produces a marked depoisoning effect upon copper sulphate, the maximum depoisoning of a 0·025 N $CuSO_4$ resulting when a ratio of 0·025 N $Cu\ SO_4$ to 0·15 N $AlCl_3$ is used. With this concentration of copper sulphate when there is less aluminium chloride present the copper sulphate is more toxic; with more aluminium chloride the poisonous effects of the latter become obvious.

By boiling the roots, Szücs was able to show by testing for copper with H_2S in acid solution that the antagonism does mean that the copper is actually not absorbed.

In a very interesting series of experiments Szücs investigated the depoisoning action of various metals on alkaloid bases. He experimented on a species of *Spirogyra.* Here also was measured the time taken for the plant to absorb enough to kill, rather than the actual time taken for death to supervene. In order to determine whether cells were alive or dead the filaments were centrifuged. If the cells are alive the chloroplasts are removed on centrifuging; if dead the plasma and chloroplasts remain fixed.

---

[1] The depoisoning of copper chloride and copper sulphate by salts of ammonium, potassium and sodium in regard to the germination of fungus spores had already been shown by Clark (6). For the depoisoning of heavy metals by lighter ones see also True and Gies (38) and Le Renard (13). Brenchley (4) has also shown that copper sulphate is much less toxic for Barley in the presence of nutrient salts than when alone in solution.

By this method it was shown that the poisoning effect of quinine hydrochloride was reduced in the presence of KNO_3 : the depoisoning effect is much more marked with $Ca(NO_3)_2$. In both these cases there is a definite ratio of alkaloid and metal which gives a maximum depoisoning effect, as above a certain concentration the metallic ions themselves become toxic. With $Al(NO_3)_3$ the depoisoning action is greatest, so that Szücs concludes that the depoisoning effect is a function of the kation valency. The same was found to be the case when methyl violet was used in place of quinine hydrochloride.

As the entrance of quinine hydrochloride or methyl violet into the cell is easily observed microchemically, Szücs was able to show that the depoisoning effect is actually due to the hindrance of the entrance of the poison. And so the toxicity of pipiridin, the entrance of which is not hindered by the presence of inorganic electrolytes, is increased rather than diminished when these latter are present.

Finally we would call attention to a recent paper by Hawkins (11) in which are recorded the results of a careful investigation of the influence of calcium, magnesium and potassium nitrates upon the toxicity of copper and other heavy metals in respect to the germination of fungus spores. The spores used were the conidial stage of *Glomerella cingulata* (Stonem.) S and v.S. It requires a considerably high concentration of nitrate of calcium (about 0·65M), magnesium (about 0·55M), or potassium (above 0·9M), to inhibit the germination of the spores, whereas a very low concentration of copper nitrate is sufficient for this (about 0·00006M). With a slightly lower concentration of copper nitrate (0·00004M) local swellings of the spore wall and swollen tubes were frequent.

Solutions of different strengths of copper nitrate (0·008M; 0·0004M; 0·0001M) were combined with calcium nitrate, and the strength of the latter determined, such that the mixed solution should produce the same result on germination as 0·00004M pure copper nitrate. It was found that the weaker the copper nitrate solution used the *relatively* smaller amount of calcium nitrate was necessary.[1] Thus for the different strengths of copper nitrate the following relative numbers of molecules of calcium nitrate were required:—

[1] Cf. Loeb's results with *Fundulus*.

$Cu(NO_3)_2$ Concentration.	$\frac{\text{Molecules of } Ca(NO_3)_2.}{\text{Molecules of } Cu(NO_3)_2.}$
0·008	6·25
0·0004	2·50
0·0001	0·63

Copper sulphate behaves quite similarly to copper nitrate. It is shewn that the result is not to be related to decreased ionisation of $Cu(NO_3)_2$ in the mixed solution, either on account of the ordinary law governing ionic dissociation in a solution of two salts with a common ion, or by the formation of a double salt only little dissociated.[1] It appears that the antitoxic action must be effective on the spores themselves.

Lead nitrate was found to be considerably less toxic than copper nitrate. Experiments were conducted in which combinations of $Pb(NO_3)_2$ of three distinct strengths (0·00016M, 0·00033M and 0·00066M) with $Ca(NO_3)_2$ were tried. To obtain mainly normal germimation with each of these three strengths a ratio of $\frac{Ca}{Pb}$ of $\frac{30}{1}$ had to be used: a result in contrast to that with copper. Magnesium was found to be about one-fifth as effective an antidote as calcium in counteracting the toxicity of $Pb(NO_3)_2$. The same relation between magnesium and calcium was found in regard to counteracting the toxicity of $Zn(NO_3)_2$.

Aluminium nitrate was found to be decidedly toxic, but in no case did the addition of either calcium or magnesium nitrate produce any effect.

Hawkins concludes that no broadly general hypothesis will explain the various antagonistic actions, and infers that the explanation of each case will have to be worked out for itself. There can however be no doubt whatever that it is by obtaining data of a quantitative nature, such as Osterhout, Hawkins, and particularly Szücs, have been attempting, that we may hope to arrive at a fuller knowledge of the meaning of antagonistic action.[2]

---

[1] It had previously been shewn by Clark (5) that the addition of small quantities of sodium chloride to a solution of mercuric chloride increased the toxicity of the solution, but that larger quantities caused a decrease of toxicity. He supposed a double salt was produced with a much higher dissociation coefficient than that of mercuric chloride.

[2] Since this paper was written Osterhout (31) has called attention to the necessity of correct criteria of antagonism, and has suggested a way in which the amount of antagonism may be measured and numerically expressed. His scheme is further developed in a later paper (32), which also promises us the publication of the results of further researches.

CONCLUSION.

From this brief survey of the work published on antagonism it is evident that we are here dealing with a phenomenon of wide-spread or perhaps universal occurrence in organic life, as it as been observed in regard to absorption by both animals and plants, and in the case of the latter in regard to species from all parts of the plant kingdom.

Antagonism appears to be limited to kations,[1] but not merely to those which are generally supposed to have a nutritive value or which are present in the plant, but, as Szücs' researches have shown, it exists also between such unnecessary or poisonous ions as aluminium and copper, and even between metals and alkaloid bases.

The cases of antagonism that have been observed so far appear to show that this effect is greatest between ions of a different valency, but it is not altogether absent between ions of the same valency.

The most plausible explanation of antagonism that has been put forward is certainly that of Szücs, which is itself based on Pauli's view of absorption.

Pauli (32) regards the plasma-membrane as acting as a carrier of ions into the interior of the cell. The plasma-membrane is supposed to form compounds with the ions and by the reversibility of the process the ions enter the cell.

Szücs points out that on this view it is possible to understand how it is that inorganic electrolytes which play so important a part in plant nutrition, but which on the other hand are insoluble in lipoids,[2] are able to enter the cell.

Szücs concludes that on Pauli's view, if there is outside the cell a mixture of salts containing two different ions, both of which are carried in by the same radicle of the plasma-membrane, these ions must naturally hinder one another's absorption; each will combine with a part of the plasma-membrane substance which would otherwise be used by the other ion if that alone were present, and so the absorption of both ions is hindered.

---

[1] However an antagonism between anions has recently been recorded by Miyake (21).

[2] It should be noted that the theory of Quincke and Overton to the effect that the plasma-membrane is of the nature of a continuous film of lipoid, is by no means generally accepted, although most workers are agreed as to the presence of lipoid in the plasma-membrane. Czapek (8) for instance suggests that the fatty substance might simply be suspended as an emulsion in a colloidal complex of water and proteid, which would enable one to understand the intake of substances like salts which are insoluble in lipoid but soluble in water.

Whereas it has been generally supposed that the seat of antagonistic ion action is the plasma-membrane, Hansteen Cranner, in a recent paper (7), puts forward the opinion that the cell wall plays an active part in the interchange of substances between the living cell and its surroundings. This author produces evidence to show that the cell wall of actively growing cells contains lipoid substances as well as cellulose and pectin, and that the cell wall must be considered as of much greater importance in the vital functions of the cell than has hitherto been supposed. A discussion of this theory lies outside the scope of the present paper. It must be left for future work to localise definitely the actual part which the various membranes surrounding the protoplast actually play in the phenomena of antagonism.

THE UNIVERSITY,
LEEDS.
June 8th, 1914.

LITERATURE CITED.

1. Benecke, W. "Über Kulturbedingungen einiger Algen." Bot. Zeit., Bd. 56, 1898, p. 93.
2. ,, "Untersuchungen über den Bedarf der Bakterien an Mineralstoffen." Bot. Zeit., Bd. 65, 1907.
3. Boehm, J. "Über den Vegetabilischen Nahrwerth der Kalksalze." Sitzungsb. d. Kais. Akad. d. wiss. in Wien. Math.-Nat. Kl. Bd. 71, 1875, p. 287.
4. Brenchley, W. E. "The Influence of Copper Sulphate and Manganese Sulphate upon the Growth of Barley." Annals of Botany, Vol. 24, 1910, pp. 571-583.
5. Clark, J. F. "On the toxic value of mercuric chloride and its double salts." Journ. Phys. Chem., Vol. 5, 1901, pp. 289-316.
6. ,, "On the toxic properties of some copper compounds with special reference to Bordeaux mixture." Bot. Gaz., Vol. 33, 1902, pp. 26-48.
7. Cranner B. Hansteen (see also Hansteen, B.). "Über das Verhalten der Kulturpflanzen zu den Bodensalzen. III. Beiträge zur Biochemie und Physiologie der Zellwand lebender Zellen." Jahrb. f. wiss. Bot., Bd. 53, 1914, p. 536.
8. Czapek, F. "Über eine Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen." Jena, 1911.
9. Gile, P. "Lime-magnesia ratio as influenced by concentration." Porto Rico Agric. Expt. Sta., Bull. 12, 1912.
10. Hansteen, B. "Über das Verhalten der Kulturpflanzen zu den Bodensalzen, I. und II." Jahrb. f. wiss. Bot., Bd. 47, 1910, p. 289.
11. Hawkins, L. A. "The Influence of Calcium, Magnesium, and Potassium nitrates upon the toxicity of Certain Heavy Metals towards fungus spores." Physiol. Researches, Vol. 1, No. 2, 1913, pp. 57-92.

12. Kearney, T. H., and Cameron, F. K. "Some Mutual Relations between Alkali Soils and Vegetation." U.S. Dept. of Agriculture, Report 71, 1902.

13. Le Renard, A. "Influence du milieu sur la résistance du Pénicille crustacé aux substances toxiques." Ann. Sci. Nat. Bot. IX, Ser. IX., Vol. 16, 1912, pp. 276-336.

14. Loeb, J. "The Dynamics of Living Tissue." New York, 1906.

15. Loew, O. "Die Bedeutung der Kalk-Magnesiasalze in der Landwirtschaft." Landw. Versuchsst., Bd. 41, 1892, p. 467.

16. ,, "Über die physiologische Funktion der Calcium- und Magnesiumsalze im Pflanzenorganismus." Flora, Bd. 75, 1892, p. 368.

17. ,, "Über die Wirkung von Strontiumsalzen auf Algen." Flora, Bd. 102, 1911, p. 96.

18. ,, and Aso, K. "On physiologically balanced solutions." Bull. Coll. Agric. Tokyo, Vol. 7, No. 31, 1907.

19. ,, and May, D. W. "The relation of lime and magnesia to plant growth." U.S. Dept. of Agric. Bur. Plant Industry, Bull. 1, 1901.

20. McCool, M. M. "The action of certain nutrient and non-nutrient bases on plant-growth." Cornell University Agricultural Experiment Station. Memoir No. 2, 1913, pp. 115-216.

21. Miyake, K. "The influence of salts common to alkali soils upon the growth of the rice plant." Journ. Biol. Chem., Vol. 16, 1913, pp. 235-263.

22. Niklewski, B. "Über den Austritt von Calcium- und Magnesium-ionen aus der Pflanzenzelle." Ber. d. deutsch. bot. Ges., Bd. 27, 1909, p. 224.

23. Osterhout, W. J. V. "On the Importance of Physiologically Balanced Solutions for Plants. I. Marine Plants." Bot. Gaz., Vol. 42, 1906, p. 127.

24. ,, ,, "On the Importance of Physiologically Balanced Solutions for Plants. II. Freshwater and Terrestrial Plants." Bot. Gaz., Vol. 44, 1907, p. 259.

25. ,, ,, "On Plasmolysis." Bot. Gaz., Vol. 46, 1908, p. 53.

26. ,, ,, "The Antagonistic Action of Magnesium and Potassium." Bot. Gaz., Vol. 45, 1908, p. 117.

27. ,, ,, "Die Schutzwirkung des Natriums fur Pflanzen." Jahrb. für wiss. Bot., Bd. 46, 1908, p. 121.

28. ,, ,, "The Permeability of Living Cells to Salts in Pure and Balanced Solutions." Science, N.S., Vol. 34, 1911, p. 187.

29. ,, ,, "The Permeability of Protoplasm to Ions and the Theory of Antagonism." Science, N.S., Vol. 35, 1912, p. 112.

30. ,, ,, "Plants which require Sodium." Bot. Gaz., Vol. 54, 1912, p. 532.

31. ,, ,, "Quantitative Criteria of Antagonism." Bot. Gaz., Vol. 58, 1914, pp. 178-186.

32. ,, ,, "The Measurement of Antagonism." Ibid. pp. 272-266.

33. Pauli, W. "Pharmako-dynamische Studien. 1. Beziehungen der physiologischen Ester- und Salzwirkung." Sitsungsb. Akad. Wiss. in Wien. mat.-nat. Kl.; Bd. 103, 1904, p. 15.

34. Sachs, J. "Über den Einfluss der chemischen und physikalischen Beschaffenheit des Bodens auf die Transpiration der Pflanzen." Landw. Versuchsst., Bd. 1, 1859, p. 203.

35. ,, "Erziehung von Landpflanzen in Wasser." Landw. Versuchsst., Bd. 2, 1860, p. 22.

36. Szücs, J. "Experimentelle Beiträge zu einer Theorie der antagonistischen Ionenwirkungen. I. Mitteilung." Jahrb. für wiss. Bot., Bd. 52, 1912, p. 85.

37. Tottingham, W. E. "A Quantitative Chemical and Physiological Study of Nutrient Solutions for Plant Cultures." Physiol. Researches, Vol. 1, No. 4, 1914, p. 133.

38. True, R. H., and Bartlett, H. H. "Absorption and Excretion of Salts by Roots as Influenced by Concentration and Composition of Culture Solutions." U.S. Dept. of Agriculture Bur. of Plant Industry, Bull. No. 231, 1912.

39. ,, and Gies, W. J. "On the Physiological Action of Some of the Heavy Metals in Mixed Solutions." Bull. Torr. Bot. Club, Vol. 30, 1903, pp. 390-402.

40. Wolf, W. "Die Saussure' schen Gesetze der Aufsaugung von einfachen Salzlösungen, usw." Landw. Versuchsst., Bd. 6, 1864.

INTERNATIONAL PHYTOGEOGRAPHIC EXCURSION (I.P.E.) IN AMERICA, 1913.

(*continued from p. 92*).

Medford and Crater Lake.

DURING the afternoon, evening and night of September 2nd we travelled southwards from Tacoma to Medford on the "Shasta Limited" of the Southern Pacific, one of the crack trains of this line, the excess fares for which had been paid by our kind hosts of the Commercial Club at Medford, Oregon, our next stopping place. Thus the hospitality of our Medford friends began before ever we arrived at their city. It was impressed upon us that during the three days on which we were the guests of the club not a single member of the party was to spend a cent, and indeed it was almost impossible to do so. It is as difficult as it would be invidious to single out the kindness and hospitality shown us at any particular centre for special appreciation, but our treatment at Medford and during the trip to Crater Lake would certainly be hard to forget.

After a rest and breakfast at the Medford Hotel, one of those luxurious and at the same time simple establishments for which the Far West is justly famed, we started in seven automobiles—most generously placed at our disposal and nearly all driven by their owners—on the 85-mile trip to Crater Lake. Medford is situated in the centre of the Rogue River Valley, a district which has recently experienced rapid development and astounding prosperity, mainly from its extensive pear orchards.

Much of the uncultivated parts of the valley plain are covered with a very stony soil supporting a poor growth of grasses such as *Hordeum* and *Aristida*, and locally known as "desert." These stony areas are probably the outwash from old glacial streams. Here and there are isolated trees of *Quercus Garryana*, a deciduous but rather leathery-leaved oak. Near the beginning of the foothills, an open scrub or "chaparral" begins, with *Ceanothus cordulatus* dominant, *Arctostaphylos glauca* abundant and occasional trees of *Quercus Garryana.* As the foothills are entered single trees of the yellow pine, *Pinus ponderosa*, appear among the chaparral, and these increase in number but do not form anything like a closed woodland. The scrub thickens and other shrubs appear, such as the beautiful *Arbutus Menziesii* and various herbs, such as the aromatic *Eremocarpus setigera* and species of *Salvia.* A marked feature of this open woodland is the great development of masses of lichen (*Usnea* and others) and mosses which appear on the tree-trunks and branches These are doubtful due to the wet and comparatively mild winters of the district.

At a somewhat higher altitude (about 2,500 feet) the Douglas Fir (*Pseudotsuga mucronata*) appears and soon increases in abundance, "chaparral" at the same time disappearing. The Douglas Fir does not, however, dominate the forests as it does in the Rockies or in the northern Cascades. The forests around Prospect, for instance, half-way up from Medford to Crater Lake consist of yellow pine and Douglas mixed with Sugar Pine (*P. Lambertiana*)—whose enormous cones, often 18 inches in length, lying on the ground, are a conspicuous feature beneath the trees—*Tsuga heterophylla, Libocedrus decurrens, Abies concolor, Taxus brevifolia* and the Lodge-pole pine (*P. Murrayana* or *contorta*), the last forming, higher up towards Crater Lake, pure stands of uniform age, springing up where the original forest has been burned. The undergrowth in the denser portions of the forest is formed of *Cornus pubescens, Corylus rostrata, Castanopsis sempervirens, Arctostaphylos* spp., *Acer circinatum*, etc. In more open forest which has been partially cleared there are often pure stands of *Ceanothus velutinus*.

On the higher slopes of the Cascades (5,000-8,000 feet) up to the rim of Crater Lake itself, subalpine forest of *Tsuga Pattoniana* with *Abies nobilis*, *A. magnifica*, *Pinus monticola*, and *P. albicaulis* occur. *Alnus sinuata*, closely allied to the European *A. viridis*, shows good alternation with *Abies* on the steep slopes of the crater leading down from the rim to the lake.

Thus there is a fine and well-marked zonation from the plain of the Rogue River valley up to the tree-limit on the Southern Cascades: (1) semi-arid grassland, (2) scrub or "chaparral," (3) mixed coniferous forest in which *Pinus ponderosa* and *Pseudotsuga* are the leading trees, with *Pinus Lambertiana*, *P. Murrayana*, etc., at higher altitudes, (4) subalpine coniferous forest with *Tsuga Pattoniana*, *Abies*, etc. This is no doubt largely determined by gradual increase of moisture as the mountains are ascended.

Crater Lake itself is a wonderful scenic feature. It occupies an immense crater caused by the subsidence of an old volcanic cone estimated to have been 14,000 feet high. The edge of the present rim reaches in places 8,100 feet, while the level of the lake below is 6,180 feet. The lake itself which has an area of more than 12 square miles, is very deep (2,000 feet in places) and its waters are fresh and very clear and blue. The atmospheric effects are wonderfully beautiful. The weather we experienced there was not all that could be desired—a gale of wind was blowing and driving rain and thick mist alternated. But the warmth of our welcome at Crater Lake Lodge was in strong contrast to the inhospitable weather.

On September 5th the party returned to Medford and were entertained to dinner by the Medford Commercial Club and the University Club of Medford—the ladies of the party by the Women's University Club. On the following morning some of the famous pear orchards, beautifully kept and cultivated, were visited under the guidance of their owners. Mr. P. J. O'Gara, who ably and enthusiastically led the party during their stay, has very largely contributed to the success of the fruit industry by his untiring efforts in counteracting plant-disease and climatic dangers such as frost. The profits made in this industry, particularly on pears, are almost incredible. The thing is done by the utmost care in cultivation and the determination to sell nothing but the best. The consequence is that the very best prices are obtained and the market dominated. The air of happy and abounding prosperity which this rapid and overwhelming success has given to the town of Medford is very striking indeed to a visitor—especially to a European visitor. Everything is new and of the best, everyone is bright, cheerful and confident.

On September 6th the last stage of the journey to San Francisco (445 miles) was entered upon. The railroad runs over the Siskiyou mountains with the magnificent snow-covered Mount Shasta constantly visible to the left. The highest altitude reached by the train is the Siskiyou tunnel at 4,130 feet. Very much the same vegetation is passed through as on the journey to Crater Lake—first grassland, chaparral and oak, the oak trees, as throughout California, often scattered singly in the dry grassland; then *Pinus ponderosa* followed by *Pseudotsuga* at the higher levels. After the first ridge is passed a very dry valley cut off from the mountain moisture is entered. Here there is dry grassland with no trees. The train again ascends to 3,900 feet, passing through fine forest with many species of pine. Then begins the final descent into the Californian plains, the zones of vegetation being passed through in the inverse order. About dusk we reached Shasta springs and soon afterwards caught our last glimpse of the magnificent snow-covered summit of Mount Shasta.

CALIFORNIA AND THE SIERRA NEVADA.

Early in the morning of September 7th we awoke to find ourselves travelling along the shores of San Francisco Bay with extensive salt marshes skirting the coast. After a breakfast and a brief stay at Oakland Station we started on the journey to the Yosemite valley, across the dry and exceedingly hot Californian plains, which are largely quite treeless, except along the streams. As the foothills of the Sierras are approached scattered trees of *Quercus lobata* appear in the grasslands and arable fields. This is a big graceful white oak 50 or 60 feet high. At Merced we changed onto the Yosemite Valley Railroad and soon began the ascent of the Merced valley. *Quercus lobata* is here replaced by the smaller "blue" oak, *Q. Douglasii*, and more or less scattered scrub begins to appear on the hillsides—at first *Adenostoma fasciculatum*, the "chamisal," with short weak needle-shaped leaves, presenting in mass a dingy green-brown colour. *Adenostoma* often forms pure sheets, alternating with dry grassland containing various species of *Avena*, with *Bromus*, *Poa*, etc. Along the streamside are willows, *Populus trichocarpa*, *Fraxinus*, and the round-leaved *Cercis occidentalis*. The chamisal soon becomes mixed with other shrubs, especially species of *Arctostaphylos* ("manzanita")—a genus exceedingly well represented in this region by a number of very closely allied species difficult to discriminate—*Cercocarpus*, *Ceanothus*, etc., which together form the dense scrub, the true Californian chaparral. Among the chaparral are seen scattered trees of *Pinus sabiniana*—the Digger Pine—a light loose-foliaged pine with very heavy massive cones accompanied by another evergreen oak, *Quercus chrysolepis*, a small tree generally 12 or 15 feet high with somewhat contorted branches and the undersides of the leaves covered with close-set golden scale-like hairs. *Q. Kelloggii*, a deciduous "black" oak, and *Q. Wislizeni*, a small dark-leaved evergreen oak, also appear. The whole aspect of the vegetation of this valley is decidedly mediterranean. The chaparral growth-forms strongly resemble those of mediterranean maquis, while *Pinus sabiniana* recalls the mediterranean *P. halepensis*, and the evergreen oaks correspond with *Q. Ilex* and *Q. suber*, though the American species are far more numerous. *Pinus ponderosa* begins to appear as single trees, though at this level—less than 2,000 feet—only small isolated trees occur. *Libocedrus decurrens* also begins to appear. In the evening El Portal—the terminus of the line and the gate of the Yosemite region, dominated by the steep and lofty hills which here shut in the canyon of the Merced river—was reached.

On the following morning—September 8th—the party continued the journey up the Merced canyon in horse-drawn vehicles. *Pinus sabiniana* and *Quercus Wislizeni* begin to disappear; *Pinus ponderosa* increases; *Pseudotsuga*, though not in quantity, begins to put in an appearance; and among other interesting trees and shrubs met with are the rare "Californian nutmeg" (*Torreya californica*), *Æsculus californica*, *Rhamnus californicus*, *Rhododendron californicum* (deciduous) and the strongly aromatic "Californian laurel" (*Umbellularia californica*).

The entrance to the Yosemite valley is flanked by the truly magnificent El Capitan rock, a practically vertical wall of granite 3,000 feet high. The valley itself is a canyon or trough with a flat alluvial floor and nearly vertical walls varying from 2,000 to 4,000 feet in height. The floor is still largely park-like with open stretches of grass alternating with stands of trees—*Pinus ponderosa*, *P. Murrayana*, *Libocedrus decurrens*, *Quercus Kelloggii*. The park-like character of the vegetation is due to the annual fires started by the Indians which kept down the forest growth. Since the district has passed under American control, these fires no longer occur and dense young stands of the conifers are springing up. The south-facing side of the valley bears *Pinus ponderosa* on the rocks and in ravines, and scrub of *Quercus chrysolepis* on the alternating talus slopes. On the top of El Capitan *Pinus Murrayana* and the subalpine species *P. Jeffreyi* occur.

In the afternoon the party drove *viâ* Inspiration Point and Chinquapin to Wawona. Magnificent views of the Yosemite with El Capitan in front were obtained in ascending the side of the valley, through forests of *Quercus Kelloggii*, *Q. chrysolepis*, *Libocedrus* and *Abies concolor* with *Rhamnus californicus*, *Ceanothus integerrimus*, *Acer macrophyllum*, and *Castanopsis* as undergrowth. On the Wawona side the forest was dominated mainly by *Pinus ponderosa* with *Libocedrus decurrens* and *Abies concolor* abundant, both showing very free regeneration. *Arctostaphylos viscida* and *A. patula* occurred in quantity in open woodland with *Cercocarpus* and *Ceanothus cordulatus* in the open and the bipinnate *Chamæbatia foliolosa* often covering the ground in great sheets. At the higher elevations near Chinquapin, *Pinus Lambertiana* increases very much, forming twenty or thirty per cent of the forest growth, and freely springing from seed, like the yellow pine and the other conifers. *Ceanothus prostratus* also appeared here. The Sugar Pine is a magnificent tree, generally exceeding 100 feet in height, and often reaching nearer 200 feet.

Wawona, at the bottom of the valley on the South Fork of the Merced River, was reached late in the evening.

The next day, September 9th, was spent in a visit to the famous Mariposa Grove of Big Trees (*Sequoia gigantea*). The forest in which the lower and upper "groves" of Big Trees occur is composed of *Abies concolor*, *Pinus ponderosa*, *Libocedrus decurrens* and *Pinus Lambertiana*, all rejuvenating well, the first-named most abundantly. The undergrowth consisted of *Ribes Nevadensis*, *Corylus rostrata*, *Cornus pubescens*; *Ceanothus cordulatus* and other species very abundant, often covering the ground in pure patches; also *Arctostaphylos patula*, *Ribes Roezlii*, *Chamæbatia foliolosa*, the raspberry-like *Rubus Nootkatensis*, *Prunus emarginata* and *Pteridium aquilinum*. The Big Trees themselves occur scattered through the woods, but particularly in groups. There are nearly 500 trees altogether in the Mariposa Forest. Though not regenerating so freely as in the groves further south on the Sierras there is quite good reproduction in places. The Big Trees are of course extraordinarily impressive both in size and height, dwarfing as they do even the great Sugar Pines, but some hours have to be spent among them before one begins to take in their grandeur, and it would be necessary to live among them before one could get anything like a full æsthetic appreciation. The most beautiful trees are those of young middle age (say 500 to 1,000 years old), whose crowns have not begun to round off. The biggest trees, whose diameter is 20 to 30 feet at the base, have a less beautiful form because of their more rounded tops, sparser branching and less dense foliage.

On September 10th the main party drove from Wawona to Glacier Point, the highest point reached in the Sierras, on the 11th came back to El Portal, and on the 12th returned to Berkeley, staying in San Francisco or its neighbourhood till September 15th.

CHAPARRAL, DRY GRASSLAND AND REDWOODS.

Sunday, September 14th, was spent in an excursion to Mount Tamalpais, on the Sausalito peninsula, which lies on the north side across the Golden Gate from San Francisco, and is ascended by electric railway. The mountain is covered with typical Californian chaparral, which has the same general ecological characteristics as mediterranean *maquis* and inhabits regions exposed to the same type of climate. Most of the trees and shrubs seen on Mount Tamalpais had already been encountered on the Sierran foothills: *Adenostoma fasciculatum*, the commonest of all the chaparral shrubs, species of *Arctostaphylos*, *Quercus Wislizeni*, *Q. chrysolepis*, species of *Ceanothus*, *Rhamnus californicus*, *Arbutus Menziesii*, *Umbellularia*, *Castanopsis*, *Eriodictyon glutinosum*, with *Heteromeles arbutifolia*, *Baccharis consanguineus*, etc. *Quercus densiflora*, a common evergreen oak of the Coast ranges, was scattered here and there. The characteristic alternation of chaparral and dry grassland with scattered oaks was seen here as elsewhere in California.

There are two views of the origin of this grassland. One is that the grassland is a primitive vegetation occupying a drier zone than the chaparral. Thus the southern slopes of the hills behind Berkeley and Oakland are dry grassland and show no tendency to produce chaparral which covers the north slopes. It has been suggested that the scattered oaks so characteristic of it increase and develop up to the limit set by the soil-water supply, which is too scanty to permit of a closed forest vegetation or even of chaparral. Whether this view be true or not, it is evident that species of evergreen oak which remain low and scrubby when growing in thick chaparral, develop into trees in the open grassland, presumably owing to freedom from root competition. The other view is that the grassland has been derived from chaparral by repeated burning of the latter, and that the oaks are relicts of the chaparral, freed from the competition of woody plants. Mr. W. S. Cooper's detailed and extensive investigation of Californian chaparral may be expected to throw much light on all these relations.

A large area of the Mount Tamalpais chaparral was burned over early in July and the vigorous sprouting from the burned stumps that had occurred by mid-September showed very well the characteristic vegetative rejuvenation of chaparral after burning.

The canyons on Mount Tamalpais are full of small redwoods (*Sequoia sempervirens*) and Douglas fir. The redwoods as opposed to the chaparral are said to be confined to the "fog region" so characteristic of the vicinity of San Francisco. The prevalence of cold mist over San Francisco city and the shores of the bay is indeed a striking characteristic, rather unexpected by the stranger. Muir Woods in Mill Valley show a very fine example of primitive redwood forest, in which the dominant tree is associated with *Quercus densiflora, Pseudotsuga mucronata, Umbellularia* and *Arbutus*, with *Acer macrophyllum, Rhododendron occidentale*, the deciduous *Corylus rostrata*, and the magnificent *Aralia californica* and *Aspidium monetum* as the great features of the undergrowth. Other abundant species are *Pteridium aquilinum, Myrica californica, Gaultheria Shallon, Vaccinium ovatum, Woodwardia radicans, Oxalis oregana*, etc., indicating of course much damper conditions, both atmospherically and edaphically than are present in typical chaparral. Apart from the dominant redwood, the whole facies of this vegetation and the leaf-form of many of the prevalent trees and shrubs is that of the "laurel type" found in the Atlantic—Mediterranean region and in the sheltered ravines of the Mediterranean foothills. In both cases the "laurel vegetation" possesses several species in common with the chaparral or *maquis*, the adjacent climatic type.

On the Yosemite trip and during the whole stay in the San Francisco region, the international party were received with true Californian hospitality and were guided and generally looked after in the most admirable way, the various local institutions—the University of the California, and the California Botanical Society—vying with one another in their efforts to give the visitors a pleasant and profitable trip. A too short visit was made by some of the party to Stanford University at Palo Alto, where Professor Campbell and Professor Peirce acted as hosts with great charm, and the beautiful buildings of the University were much admired. To Professors Setchell, Jepson and Hall, and to Miss Alice Eastwood, the party were greatly indebted for their kindness during the stay as a whole.

(*to be continued*).

NOTES ON *BATRACHOSPERMUM.*

BY S. REGINALD PRICE, M.A.

[WITH TEN FIGURES IN THE TEXT].

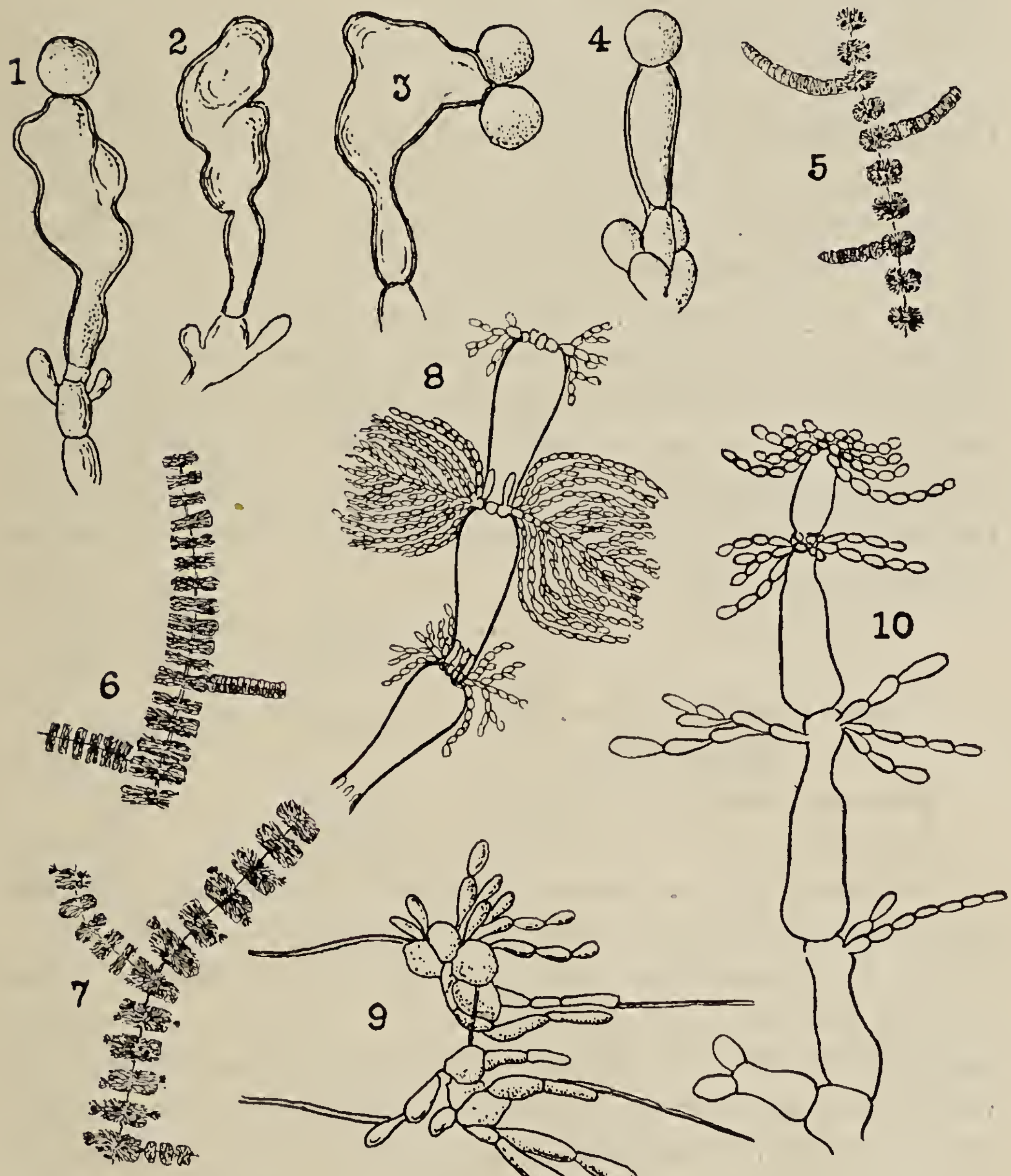
MATERIAL of *Batrachospermum moniliforme* was collected for use in class in October, 1913, by Mr. Shrubbs. This was from a fresh locality at Sawston, Cambridgeshire, the streams at Fulbourne where it has been usually obtained having been drained by well-boring operations. This material was found to show considerable differences from that usually regarded as *B. moniliforme*, and a further examination of it was made. In February of the present year more material was gathered from the same spot, and it was found to have spread very considerably in the stream during the interval. This material was compared with the former samples and with others from different localities. It may be noted that *B. atrum* was also found in the same stream, in sparing quantities.

The most striking feature of the October material was the presence of large numbers of peculiarly contorted and considerably hypertrophied trichogynes (Figs. 1-3). These were practically universal on the dark-coloured plants which were plentiful in the material, the other paler and more delicate plants having the typical *B. moniliforme* type of trichogyne (Fig. 4). Various examples of these trichogynes are figured, with a typical one of *B. moniliforme* on the same scale.

Bent trichogynes have been found occasionally, and one slightly bent is figured by Sirodot[1] for *B. testale*, but Professor West tells me that he has never seen them all bent as in this material. The trichogynes seem to be functioning normally, for spermatia were attached in many cases, and carpogonia were frequently developing. No signs of any attacking fungus or animal which might have caused the hypertrophy were found. In the material collected in February, the general external appearance was very similar, and few trichogynes were present (carpogonia being very abundant); these trichogynes were generally of the normal type, although a few were slightly elongated. Variations in the general

[1] Sirodot, L. "Les Batrachospermes." Paris, 1884, Pl. 42, fig. 7.

growth form of the thalli were also very frequent, a series of merging types being found. They varied in colour from a pale green in the typical *B. moniliforme* to a dark olive green in some types, especially in that which somewhat resembles Sirodot's figure of *B. Corbula*—see Fig. 6, and compare Sirodot, Plate V, fig. 1.



FIGS. 1—10. *BATRACHOSPERMUM.*

Figs. 1–3, camera lucida drawings of three hypertrophied trichogynes illustrating the varied and peculiar forms, spermatia were actually present as figured. Fig. 4, a normal trichogyne of *B. moniliforme*, figured on the same scale. Figs. 5–7, three types of growth form drawn with slight magnification. Fig. 5, typical *B. moniliforme*. Fig. 6, a type appearing externally somewhat like *B. Corbula*, Sirdt. Fig. 7 has a large central axis and discoid verticels. Fig. 8, central axis showing the inflated cells nearly destitute of a cortical covering, the cells are enlarged towards the basal end. Fig. 9, the slight development of the cortical filaments as in Fig. 8, shown in detail. Fig. 10, a central row of a branch of verticel, which bears a cystocarp at the apex, the form of the cells is like that of the corresponding rows in *B. Corbula*, Sirdt.

A few of these types are figured (Figs. 5-7) from drawings made with a simple lens on approximately the same scale; further description of these types is unnecessary.

Other features of interest were made out in the structure of the axis and form of the thallus, and here there seemed to be considerable variation in the material.

The most striking variation was in the dark olive-black material collected in October. In this the axial cells were generally much larger than in the paler material (typical *B. moniliforme*), inflated at one end and practically without cortex. Professor West kindly sent me some material which he regarded as type *B. moniliforme*, and this was practically identical in characters with the "*B. moniliforme*" of my material. I can find no descriptions of such a central axial row of cells in Sirodot, who studied these variations very closely, or in De Toni's "Sylloge Algarum." Fig. 8 shows a few axial cells of such a form, and Fig. 9 the slight growth of cortical filaments at the bases of the verticels. These cells, even on the fairly old axes, were quite short. The following measurements give the general proportions.

Wide Axial Cells	80-110μ	or more	wide.
	180-300μ	,,	long.
Typical *moniliforme* Prof. West. Rather small.	20-30μ	,,	wide.
Ordinary Material (February)...	60-90μ	,,	wide.
	500-600μ	,,	long.

In general the central row seems to be practically cylindrical and comparatively slender when compared with this material.

In February, other types of material were found. These differed considerably in external form, and one type seems to approach Sirodot's *B. Corbula*. These growth forms are probably not distinct, however, and they seem to merge into one another.[1] The axis here is often inflated considerably at one end, but the cells are much elongated, and the cortex only partially covers the cells even at this stage. It would appear somewhat as if these axes represent axes corresponding to the Autumn material, of which the cells have increased considerably in length. There seems, however, to be practically every stage of axis form leading from this to that associated with typical *B. moniliforme*.

In the material like *B. Corbula*, Sirdt. also lateral axes of the verticels with very much enlarged cells occurred, each bearing a carpogonium (glomérule) at the top (see Fig. 10) and cf. Sirodot (*l.c.*, Pl. V, Fig. 2). In this direction also variations of this type are found, leading to the ordinary small-celled axis.

---

[1] cf. De Toni, Vol. IV. Sect. 1, p. 50.

The *B. atrum* found was absolutely distinct in characters from these.

It thus appears probable that a series of growth forms of *B. moniliforme* have been examined, and that under certain conditions *B. moniliforme* is an extremely variable species, as of course is well known, but that these forms are probably not definite enough to merit the name of species or even of true varieties.

The presence of a type somewhat like *B. Corbula* indicates, as Professor West suggested, that probably many of Sirodot's species are really growth forms of a few common species.

No explanation of the hypertrophied trichogynes is at present forthcoming, but it is hoped that the locality may be watched to see if they reappear from time to time.

I desire to express my thanks to Professor West for his kindness in examining some of the material and looking through the manuscript.

THE BOTANY SCHOOL,
CAMBRIDGE.
April, 1914.

REVIEW.

THE SALTON SEA: A STUDY OF THE GEOGRAPHY, THE GEOLOGY, THE FLORISTICS, AND THE ECOLOGY OF A DESERT BASIN.

By D. T. MacDougal and Collaborators. Washington: Carnegie
Institution, Publication No. 193, 1914; pp. ix and 182;
32 collotype plates.

THIS sumptuous volume contains the results of an elaborate piece of co-operative research undertaken by the workers at the Desert Laboratory, Tucson, and carried on systematically since 1907. Brief interim reports of progress made in various branches have been published in the annual reports of the Director of the Laboratory, Dr. D. T. MacDougal, and now we have a detailed account, illustrated by numerous fine plates, of the results obtained by the investigation from various points of view of the phenomena presented by a desert basin which has been the scene of alternate submergence and desiccation.

The Cahuilla Basin, lying to the west of the lower (southern) part of the main delta of the Colorado River, was in Tertiary times cut off by this delta from the free access of the sea and so became an inland lake (Lake Cahuilla) of salt or brackish water. The lake-bed, called the Salton Sink, has its upper margin about 20 feet above mean tide-level, while its lowest point, now beneath the water of the present lake (Salton Sea), is 280 feet below this level. On either hand of the Sink, which is oblong in outline (about 80 miles long and 30 miles in greatest width), there rise arid and sun-scorched low mountains, whose slopes and waterless cañons bear a scanty but interesting vegetation—not dealt with in this work. The Sink is practically a level plain, everywhere exposed to equal insolation, with no irregularities of surface serving to vary the effects of sun and wind, with a uniform temperature and uniform deficiency of atmospheric humidity and precipitation (average 2·74 inches, but varying from 7·1 inch to 0·01 inch per annum during 36 years). The ancient lake which originally filled the Sink had almost or entirely disappeared by evaporation, leaving a series of beach-lines, but during 1905 and 1906 the cutting of canals and the resulting unforseen escape from control of the Colorado River-water resulted in a partial reflooding of the basin and the formation of the Salton Sea. The body of water which threatened the restoration of the former lake-conditions had in 1907 attained an area of over 400 square miles, with a maximum depth of 80 feet, submerging railway stations and necessitating the removal of the Southern Pacific railway-track for 67 miles to a higher level. But in that year the engineers in charge stopped the deluge by re-diverting the escaped waters of the Colorado River to the Gulf of

California. The gradual disappearance of the Salton Sea by evaporation then began and is now in progress. Since 1907 the average annual rate of lowering of level by evaporation has been about 5 feet.

The first three chapters deal with the geography, geology and soils of the Cahuilla basin, that written by the late Professor W. P. Blake being of special interest from the fact that it is based on observations begun with his discovery of the basin-like character of the region in 1853 and extended to his last visit in 1906. Mr. G. Sykes deals in detail with the geographical changes recorded in the drainage system of the area. Mr. E. E. Free distinguishes two main types of soils—desert soils derived from the granitic rocks of the surrounding mountains and consisting mostly of unweathered angular fragments, and alluvial delta soils which are heavy and muddy silts or fine sands. The silty soils are alkaline owing to the accumulation in the surface-layers of excessive amounts of soluble salts, mainly chloride and sulphate of sodium, this accumulation being essentially a desert phenomenon due to the natural movement of water through the finer soils being too slight to remove the salts set free by decay of the soil minerals. Since in the sandy soils the capillary forces are too weak to allow reascent of rain-water to the surface, these soils are never alkaline unless the natural drainage is insufficient. Two interesting points are brought out in connexion with the alkalinity of the soils. The submergence of the soils by the Salton water seems to have had surprisingly little effect upon their alkali content, evidently because when the water retreats it does so slowly and the underground water-table lags considerably behind the actual water-line. In this way the soil after emergence remains long wet and has Salton water continually supplied to it by outward diffusion from the Sea and subsequent capillary rise. At the same time evaporation is intense and the Salton water brackish, and under these ideal conditions for the rapid accumulation of alkali, what alkali is leached out by the Sea will be restored, or more than restored, on its retreat. The second point is that the soils appear to have surprisingly slight influence on the distribution of vegetation; it was found impossible to correlate the distribution of the beach vegetation with any variation of soil or soil-alkali.

Mr. W. H. Ross reports on the chemical composition of the water of Salton Sea and its annual variation in concentration between 1906 and 1911. The annual increase in concentration has been fairly uniform during this period, and the proportion of total solids has now risen to a little over 1%. A table is given comparing the composition of the Salton Sea-water with that of other natural waters, and showing that the waters listed may be divided into four groups:—(1) chloride waters in which sodium chloride is the chief constituent, *e.g.*, ocean water and that of Great Salt Lake; (2) chloride-sulphate waters in which both chlorides and sulphates predominate, *e.g.*, Caspian Sea; (3) chloride-sulphate-carbonate waters which contain notable amounts of carbonates as well as sulphates and chlorides, *e.g.*, Salton Sea; (4) natural salt-pans in which prolonged evaporation has brought about a concentration of the bromides and the soluble potassium and magnesium salts, while the less soluble sodium chloride and the carbonates and sulphates of calcium have mostly crystallised out, *e.g.*, Dead Sea.

The remainder of the volume (pp. 49-182) is devoted to the biological results obtained. Professor G. J. Peirce gives a most interesting account of the behaviour of the micro-organisms found in the Salton Sea and especially in the strong brines from which salt is crystallising out. He remarks upon the surprisingly large number of plants and animals living under what are commonly supposed to be fatal conditions, *e.g.*, the mould-fungi which thrive on solutions of strychnine, formalin, carbolic acid, etc., the insects in oil-wells and asphaltum, the organisms in extremely cold and extremely hot waters. In these cases, however, conditions are fairly stable, and it is harder to understand how organisms like the brine shrimps (*Artemia*) and the lowly Flagellata and Algæ found in the Salton Sea and other strong brines can exist under conditions ranging from rain-diluted sea-water to concentrated brine from which common salt crystallises out, and even survive enclosed in the salt crystals. The plants upon which the brine shrimps and Protozoa of the Salton Sea feed are mainly two species of *Dunaliella*, with allied forms like *Pyramimonas* and *Carteria*, and various bacteria. The putrefactive bacteria found in waters of the usual concentrations are killed by concentrated brines, hence the decay which goes on in these brines is accomplished by entirely different bacteria, one at least of which is chromogenic, giving a red colour to the brine itself, the salt obtained from it in the salterns, and fish pickled with this salt. A series of tables is given showing the behaviour of the organisms under different conditions and the extraordinary composition, as to both quality and quantity of the medium in which these organisms live. Professor Peirce remarks upon the difficulty of understanding how any sort of balance, osmotic, adsorptive and chemical, is maintained against such odds. Besides being a concentrated solution of sodium chloride, the brine is also a concentrated solution of magnesium salts and contains a considerable proportion of potassium. "Between the proportion of calcium and magnesium in concentrated brines and the mother-liquor there can be no 'balance'; but since, in other respects than lack of 'balance,' these solutions are fatal but inhabited, they throw no real light on the value of the idea of 'balanced solutions' and only continue, if they do not justify, natural scepticism regarding it."

Further reports, evidently intended as preliminary to more detailed investigations, on the action of micro-organisms in Salton Sea are contributed by M. A. Brannon and J. C. Jones, the former dealing with the destruction of the tissues of woody plants—submerged by flooding of the Sea—by the agency of bacteria of the Amylobacter group, and the latter with the part played by *Calothrix* and other Algæ in the formation of tufa deposits.

The next chapter (pp. 85-114) is occupied by what is described in the Preface as "a description of the plants which form the vegetative setting of the drama of the appearance and disappearance of the lake," by S. B. Parish. In this chapter on the plant ecology and floristics of Salton Sink, Mr. Parish deals with the vegetation of the area lying between the margin of the prehistoric Lake Cahuilla and that of the present Salton Sea. After discussing the position occupied by the flora of the Sink to the general scheme of plant-distribution of the Colorado Desert, Mr. Parish notes that with the climatic variations eliminated or negligible, owing to the uniform topography of the Sink, the question of distribution is left dependent directly upon the chemical and mechanical character of the soil and its water-content. Five "formations" are distinguished—hydrophytic, helophytic (always printed "heliophytic"), halophytic, mesophytic and xerophytic. The hydrophytes are very feebly represented, the water of the rivers and canals being so heavily silt-loaded as to prevent the growth of aquatics, and the amount of clear water being very limited; only in one place was a submerged seed-plant observed, the bed of a shallow stream being filled with a thick growth of *Ruppia maritima.* The helophytic formation is considered under two associations, that of springs at the upper or northern end of the Sink consisting of *Typha latifolia* and *Scirpus olneyi,* that of the rivers and canals at the lower or southern end of *Typha* with *Scirpus paludosus* and *Cyperus erythrorhizos.* The halophytic associations are much more extensive and cover large areas of the alkaline mud-flats; the dominant plants are almost everywhere Chenopods. Those parts of the flats where the alkaline content exceeds the amount tolerated by the *Atriplex* spp., are occupied mainly by species of *Suæda* and *Spirostachys.* As may be inferred from the climatic conditions, mesophytes are poorly represented and show certain xerophytic features; they are mainly cottonwood *(Populus macdougalii), Salix* spp., and *Baccharis glutinosus*—all small—or narrow-leaved forms. The xerophytic vegetation of the Sink is a part of the general flora of the Colorado Desert, differentiated mainly by the great preponderance of species of *Atriplex* in its composition, and this formation occupies an area exceeding the combined areas of all the others, comprising, indeed, the greater part of the whole Sink. The xerophytic flora of the area is remarkably uniform, though showing three associations dependent on the nature of the several soils and distinguished as the associations of detrial slopes, of the clays, and of the mounds of loose drifted materials found in different parts of the Sink. The total flora of the Sink consists of 202 species, of which 179 are seed-plants. Of the 79 xerophytes found, 51 are common in some parts of the Sink, and two are abundant everywhere in the arid soils and in the physiologically dry alkaline soils—these two, *Atriplex canescens* and *Isocoma veneta,* probably equal in number of individuals the united total of all the other plants above the rank of herbs. Six species of seed-plants are endemic in the Sink.

The longest chapter (pp. 115-172) is that by Dr. MacDougal, dealing with the movements of vegetation in the area. The chief interest in this chapter "centres in the fate of organisms overwhelmed by floods, in the physical changes which follow emersion, and in the biological mechanism of re-occupation of sterilised areas as they emerge from the water—episodes which must have been duplicated in their main features innumerable times in the history of the surface of the earth." As the author points out, opportunities for studies of this kind, and for analysis of the means and manner by which organisms colonise a sterilised area, are not common. The phenomena observed on the emersed lands of the Salton area are widely different from those investigated for Krakatau (Treub, Ernst, Campbell), the lavas of the Hawaiian Islands (Forbes), newly made land about the mouth of rivers (Oliver, Flahault and Combes), and so on. The chief features in the re-vegetation of the beaches are summed up by the following "reduction of the field notes to a history of the strands or zones emersed during each year of the recession of Salton Sea." (1) The lake rose quickly to its maximum level and receded quickly. (2) The infiltration and leaching of the soil varied year by year as affected by the concentration of the water on one hand and the time of submergence on the other. (3) The salt content of the water, least during 1907, increased by 18 to 20 per cent. in each succeeding year. (4) Each emersed strand would therefore be saturated with a soil solution resulting from the infiltration of lake water of the concentration and composition prevalent in the period preceding emergence. (5) The desiccation of the emersed strands would proceed at a rate determined by the character of the soil and by the composition of the infiltrated water. (6) The rising water of the lake picked up seeds lying on the surface, and their survival constituted a means of re-vegetation, chiefly of the strand bared in 1907. (7) The rates of evaporation and of recession of the lake varied with the season, the total evaporation being estimated at 116 inches per year, while the average rainfall was 2·74 inches per year. (8) Rapid recession of the water would result in separating stranded seeds quickly from the margin of the water, and rapid desiccation of the surface layer of soil, which would be unfavourable to germination and survival. (9) The shallow water lying on mud flats fringing the shores was raised to a much higher temperature (15° to 20° F.) than the body of the lake, even during the winter season, thereby greatly increasing its toxicity for seeds, seedlings and propagating bodies generally; most of the seeds falling into the lake would be subjected to this action. The muddy flats fringing the shores at all stages of the lake must therefore be considered as a barrier which would be crossed by a plant carried out into the lake and again when deposited on a beach.

Details are given of the invasion of the strands formed from 1907 onwards, and the behaviour of the invaders. Most of the plants invading the strands were carried there as seeds by the wind, by flotation, or by birds. Observations on the subsequent behaviour of the vegetation of the strands during the succeeding years up to 1913, with special reference to such topics as the influence of the lake on the vegetation of the dry slopes above its level, the endurance and survival of seeds and plants, the biological and physical conditions of dissemination and reoccupation, the flotation and germination of seeds, the processes of succession and elimination, and the reoccupation of emerging sterilised islands, make up the remainder of this interesting chapter.

Dr. MacDougal and his collaborators are to be warmly congratulated upon this valuable scientific study of a set of phenomena which gives opportunity for the investigation and discussion of so many topics of ecological importance.

F.C.

THE
NEW PHYTOLOGIST.

VOL. XIII, NO. 9. NOVEMBER, 1914.
[PUBLISHED NOVEMBER 30TH, 1914.]

A REVIEW OF LITERATURE CONCERNING THE EVOLUTION OF MONOCOTYLEDONS.

BY N. BANCROFT.

[WITH FOUR DIAGRAMS IN THE TEXT.]

I. INTRODUCTION.

WHAT is the position of Monocotyledons in a natural system of classification—that is, a system which takes into account the probable evolution of the group and its relationship to other forms? This is a question of considerable interest, and one which has given rise, particularly of late, to various theories of the primitive or derived nature of monocotyly, and to many phylogenetic schemes.

II. OLDER CLASSIFICATIONS AND VIEWS OF THE POSITION OF THE GROUP.

John Ray (55), whose "Historia Plantarum" was published between 1686 and 1704, was the first systematist to base his classification of flowering plants on the presence of one or two cotyledons in the embryo. This character provided a convenient method of grouping, and has been used by the majority of writers since Ray's time. It is very possible, that in framing their systems of classification, even the earliest botanists had some underlying ideas of *degree* of development (though not necessarily of phylogenetic or evolutionary development), and also of relationship between their plant-groups; and it is therefore interesting to note that in the majority of cases since Ray's time, Monocotyledons are placed *before* Dicotyledons, or between that group and the flowerless plants.

For example, the younger de Jussieu published in 1789 (15) a classification which may claim to be the first complete and natural system. He proceeds from Acotyledons (Cryptogams) to Dicotyledons, making Monocotyledons an intermediate class. DeCandolle's system, published in 1819 (14), considers first Dicotyledons, then Monocotyledons (including Cryptogams), and lastly cellular plants, foliaceous and non-foliaceous, Monocotyledons again appearing between the higher and lower forms. The systems of Endlicher (1836–1840) (19) and Adolphe Brongniart (1843) (8) again indicate the general tendency to consider the Monocotyledons as a less highly developed group than the Dicotyledons, and nearer the lower or flowerless forms.[1]

This view is illustrated by Campbell (9, pp. 196–198) who in his "Lectures on the Evolution of Plants," published as recently as 1899, postulates the derivation of Monocotyledons from Pteridophyte ancestors (or "possibly through forms related to the Cycads"). The Monocotyledons in their turn, he believes, lead to the Dicotyledons through two lines, the Aroids and the Apocarpæ.[2]

A notable exception to the above tendency among the older classifications may be mentioned: Linnaeus (41), in his "Philosophia Botanica" (1751), arranged the genera he had established in sixty-seven orders, losing sight, apparently, of the distinction between Monocotyledons and Dicotyledons—at least he does not mention it. It is an interesting fact, however, that his first fourteen orders, with the exception of the twelfth (and this includes *Magnolia* and *Liriodendron*[3]), consist almost entirely of monocotyledonous forms, some of the orders representing natural groups, such as Palmæ, Gramina and Orchideæ. The last orders in Linnaeus' system consist of ferns, mosses, algæ and fungi; so that it appears as if he considered the first orders to contain the highest forms—that is, those of a higher degree of development.

Before passing on to the newer schemes of classification, mention should be made of Agardh's grouping of the embryos of flowering plants (Diagram I). In his text-book of 1829–1832, he groups the embryos under the two main headings of Dicotyledons and Kryptocotyledons (1, p. 197). His Dicotyledons include *true* Dicotyledons—that is, all the forms we now consider as Dicotyledons, except the Nymphæaceæ—and Polycotyledons, namely Conifers.

---

[1] See Rendle's "Classification of Flowering Plants," (56), Chap. I, for further information on these and other systems.

[2] Cf. the exactly opposite view of Lotsy (42, p. 10).

[3] A suggestive point, considered in the light of recent research.

His Kryptocotyledons consist of Monocotyledons, a sub-group containing the Gramineæ only; and Syncotyledons, which include the Blieæ, Aroideæ, Naiadeæ, Palmæ, Scitamineæ, Nymphæaceæ and Cycads. The interest of Agardh's classification consists in the fact that he considers the dicotyledonous embryo as typical, and the syncotyledonous embryo as derived from it by the fusion of the two original cotyledons. Agardh further regards the grasses as the only true Monocotyledons, the embryo in this case being derived from a dicotyledonous type by the suppression of one seed-leaf.

Suggestive as this idea of the monocotyledonous embryo is, in the present connection, it is perhaps only fair to note that Agardh's classification was probably founded on a misconception of the nature of the endosperm in the Monocotyledons (excluding the Gramineæ) and in the Nymphæaceæ (cf. Sargant, 59, p. 71).

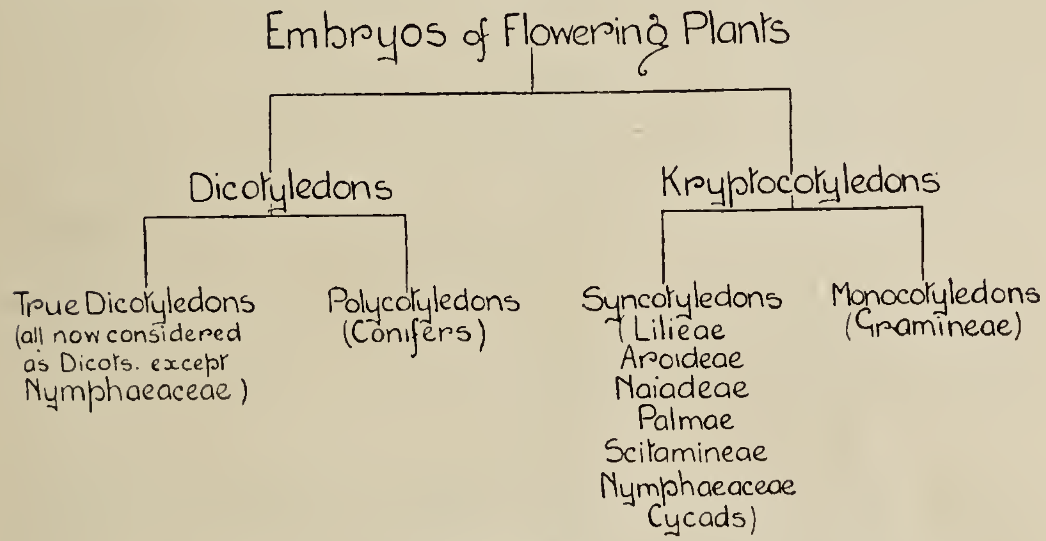

Embryos of Flowering Plants
Dicotyledons
Kryptocotyledons
True Dicotyledons (all now considered as Dicots. except Nymphaeaceae)
Polycotyledons (Conifers)
Syncotyledons (Lilieae Aroideae Naiadeae Palmae Scitamineae Nymphaeaceae Cycads)
Monocotyledons (Gramineae)

Diagram I.

A Classification of the Embryos of Flowering Plants according to Agardh (1829–1832).

III. Newer Classifications and Phylogenetic Schemes.

The idea that the Monocotyledons represented an older, more primitive or less highly-developed group was generally accepted until perhaps a little more than a generation ago. In more recent years, however, there has been a breaking-free from the far-reaching influence of Linnaeus, whose artificial system of classification, and belief in the "special creation" theory did much to check advance in the study of plant relationships. Morphological and anatomical studies have produced ideas as to the probable phylogeny of the plant-groups, together with more natural schemes of classification. Amongst these later systems may be mentioned those of Bessey (7; see also 6), Engler (21), Wettstein (75), Lotsy

(42), Warming (74) and Hallier (26, 27, 28). These may be considered briefly with regard to their treatment of the two main divisions of the Angiosperms.

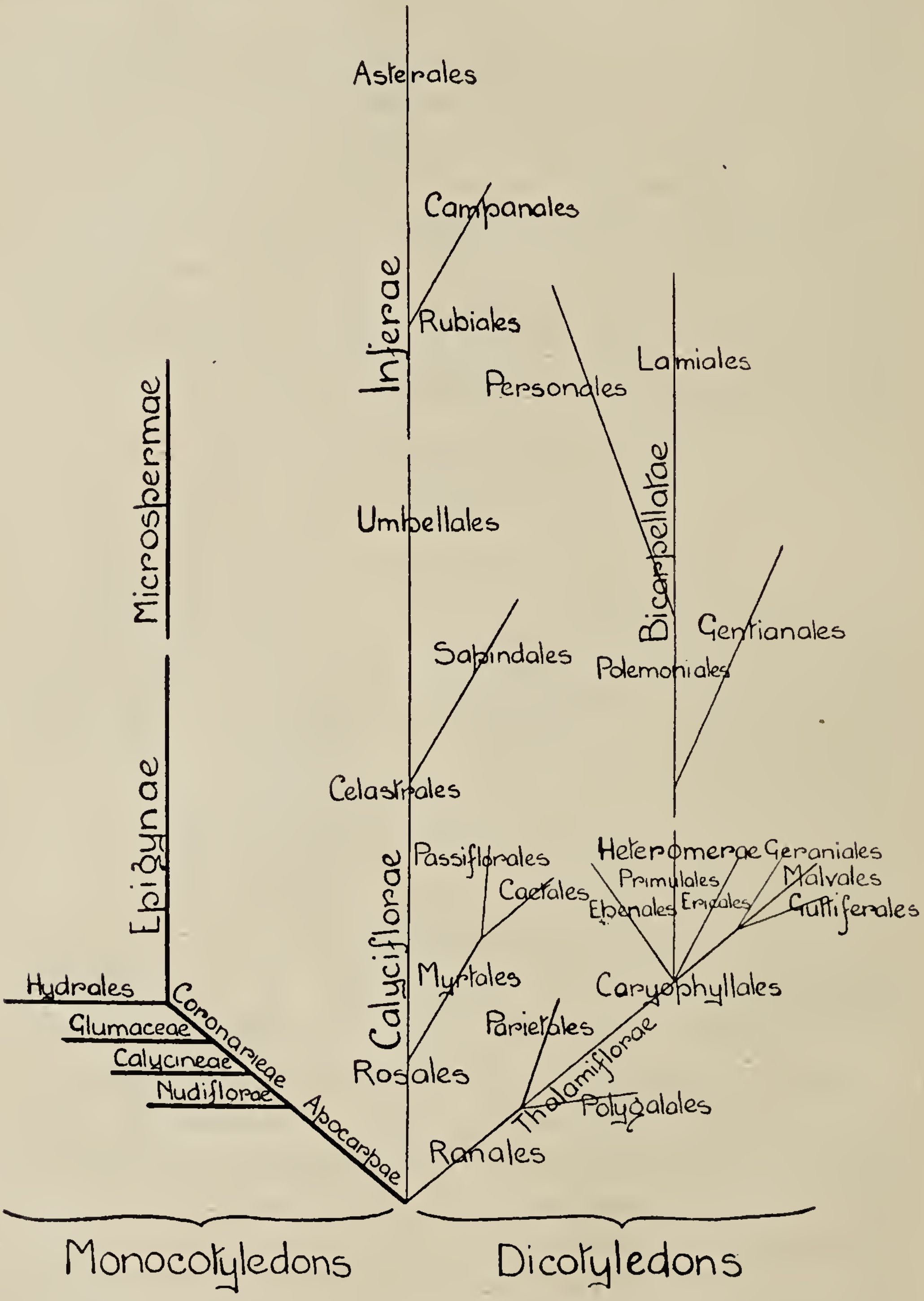


Diagram II.
The Evolution of the Monocotyledons according to Bessey's System (1897).

Bessey (Diagram II; see 7) considers that Monocotyledons and Dicotyledons are modifications of a common type, diverging from one another at an early period, the apocarpous forms of both groups being the most nearly related.[1] There is no evidence that either group was derived from the other, but there are, according to Bessey, structural indications that Monocotyledons must rank lower than Dicotyledons. He believes that the earliest forms of both groups made their appearance almost simultaneously in late Permo-Carboniferous or early Mesozoic times, but palæobotanical investigations show that there is no actual reliable evidence for the presence of Angiosperms before the Cretaceous,[2] though both sub-groups appear to be well-established by the end of that period, according to the work of Drs. Stopes and Fujii (67, 68). A recent paper by Horwood (36) gives a useful summary of fossil Monocotyledons, showing that the first authentic specimens are from the Cretaceous. Horwood agrees with Bessey in believing that Monocotyledons and Dicotyledons arose from a common ancestor, resembling an Alismaceous or Liliaceous type on the one hand and a Ranalean type on the other.

Engler (21) deals with the Monocotyledons before the Dicotyledons, explaining that he leaves them in the position they have generally held in previous classifications, because he does not consider that there is sufficient evidence for the growing idea of their derivation from Dicotyledons. He prefers to regard them as two groups of equal value (21, p. vi of preface). Of the phylogeny of the Angiosperms as a whole, he gives very little idea, but considers both Monocotyledons and Dicotyledons as being polyphyletic (20, pp. 371–380).

Warming (74) also places the Monocotyledons first in his system, and follows Engler in preferring, in the present state of our knowledge, to consider Monocotyledons and Dicotyledons as two independent lines of evolution.

It may be remarked before passing on to other systems that this view of independence of the two groups was suggested as early as 1875 by Kny (37, p. 61). It was held by Drude (17, pp. 184, 304) and has had various supporters who have set forth their ideas of phylogeny more or less definitely. For example, Coulter and Chamberlain (12, pp. 284, 285) derive the Monocotyledons from an *Isoëtes*-like ancestor, and the Dicotyledons from a *Selaginella*-like type on the grounds of similarity of the embryos. As an alternative they suggest that both came from extinct lines of Eusporangiate

---

[1] Cf. Fritsch (23). This author believes that the Ranales and Helobieæ had a common origin in extinct and unknown forms.

[2] Cf. Scott (64, p. 660); Seward (65, p. 220); Coulter and Chamberlain (12, p. 273).

Heterosporous Filicales.[1] Fritsch (23) considers Monocotyledons and Dicotyledons to be two independent groups having evolved from a common ancestor, extinct and unknown, by way of the Helobieæ and Ranales respectively, or having had separate origins in extinct Gymnosperms or Pteridophyta. Lindinger (40; see also 39), in 1910, has been one of the most recent exponents of the "independence theory." From a consideration of root and stem-structure in Monocotyledons, he concludes that this line is independent so far as the Dicotyledons are concerned; nor can any connection be traced with known Gymnospermous types, recent or fossil. In considering the characters of the primitive Monocotyledon, Lindinger mentions *Dracaena*, *Aloë* and *Yucca* as having retained ancestral characters in the purest form—an interesting point in connection

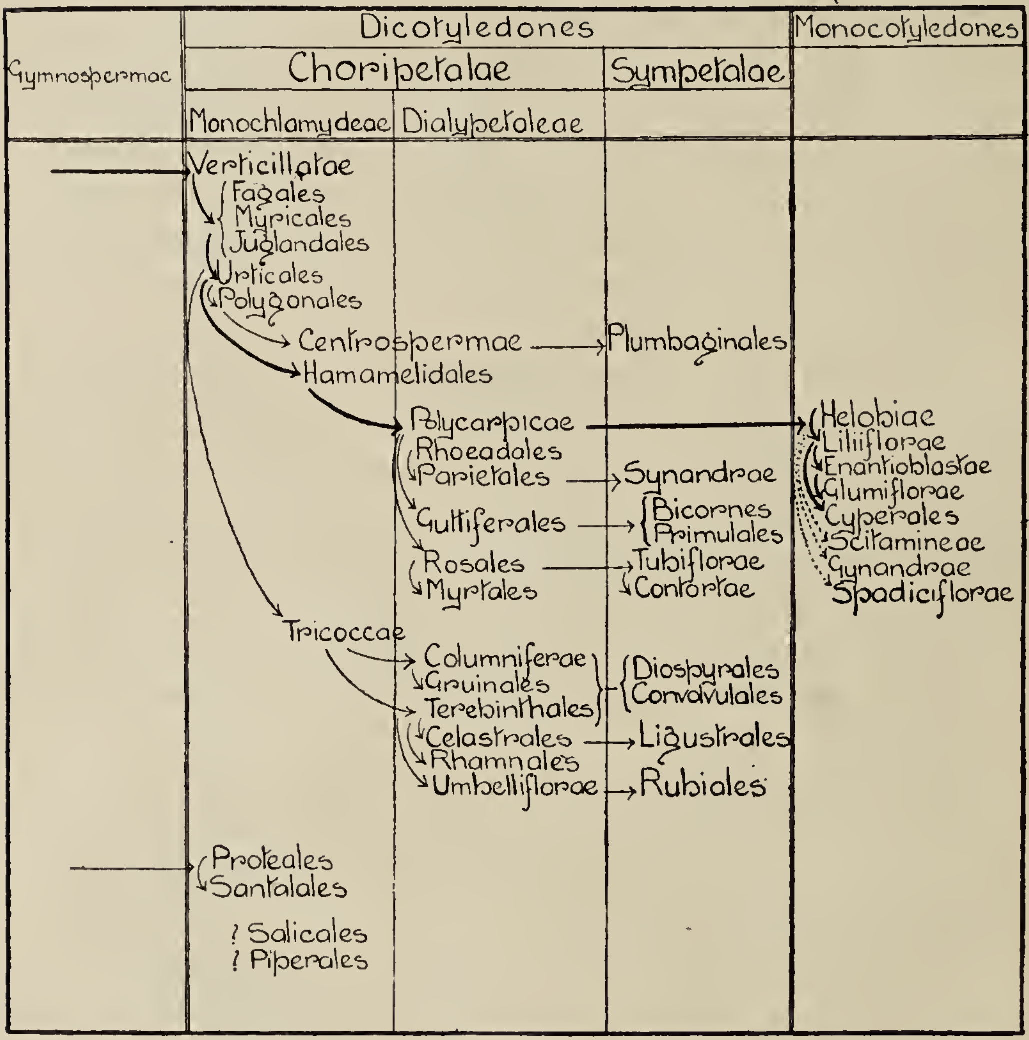


DIAGRAM III.
The Evolution of the Monocotyledons, according to Wettstein's System (1911).

---

[1] They admit, however, that "the arguments in favour of the monophyletic origin of Angiosperms are strong; and if this view be accepted, the derivation of Monocotyledons from primitive Dicotyledons seems to rest on stronger evidence than the reverse relationship" (p. 288).

with the idea of the primitiveness of the arboreal habit (cf. 5, 10, 18). He contends that while the Angiospermous condition may be regarded as an argument for intimate relationship between the two groups, this condition may have arisen more than once, in the same way as did the seed-habit.

According to Wettstein (75, p. 865), the Angiosperms are monophyletic, or possibly diphyletic (Diagram III). The chief point of his system in the present connection is that he derives all the Monocotyledons through the Helobieæ from the Polycarpicæ (a group corresponding broadly to Engler's Ranales). The Polycarpicæ in their turn he considers as having descended from Gymnosperms by way of the Monochlamydeæ, as the diagram shows.

Lotsy (42, pp. 863, 864) also believes that the Dicotyledons are the older type (Diagram IV), but he derives the Monocotyledons from them at two different points—the first in the neighbourhood of the Piperales, through which the Spadicifloræ are considered to have evolved; and the second in a hypothetical group, the Proranales, from which lines of evolution are traced to the Liliifloræ and Helobieæ. A similar diphyletic view of the origin of Monocotyledons was suggested by Hill in 1906, in a paper on Piperalean seedling-structure (33, pp. 173, 174). According to Lotsy, the whole of the Angiosperm phylum is derived from the Bennettiteæ by way of a hypothetical Proangiosperm ancestor.[1]

Hallier (26, 27, 28) has advanced a system which he varies in different degrees from time to time—as Lotsy remarks, it is free from the reproach of being too rigid. In all his variations, however, he treats the Dicotyledons as the older form and derives them from Cycadophyte ancestors. The Monocotyledons he refers to ancestors amongst the Polycarpicæ, which group he gives thirty-two reasons for considering as primitive.

With regard to the primitiveness of the Polycarpicæ and their relation to the Monocotyledons, the following investigations are of interest. Fries (22) in studying the leaf-arrangement on lateral axes, found that among the Anonaceæ and Nymphæaceæ, the Monocotyledon type, in which the first leaf is adaxial to the main axis, is more common than the Dicotyledon type, in which the two first leaves are transversely placed (see 22, fig. 1, p. 294). Mez and Gohlke (48), from serological investigations, decide that the Magnoliaceæ include the most primitive Angiosperms, and that the Alismataceæ, Butomaceæ and Juncaginaceæ are primitive among Monocotyledons.

[1] Cf. Arber and Parkin (2) and Hallier (27).

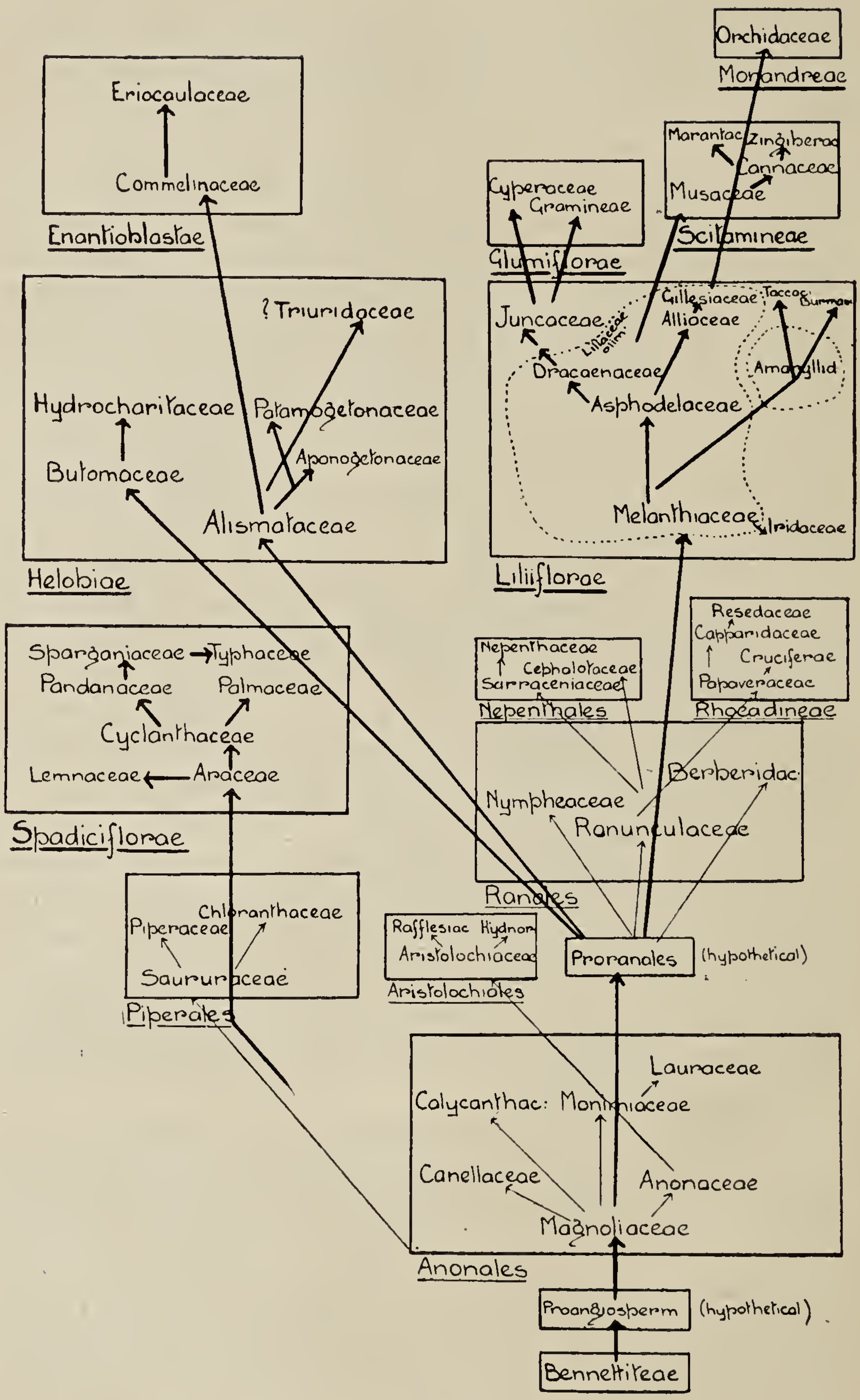


DIAGRAM IV.
The Evolution of the Monocotyledons, according to Lotsy's System (1911).

Alisma reacts serologically to *Magnolia*, thus showing, according to Mez and Gohlke, direct relationship between the two forms.[1] Maneval (47) has recently studied the development of *Magnolia* and *Liriodendron*, and concludes that the Magnoliaceæ or related forms represent the most primitive of existing Angiosperms. Porsch (54, p. 589) sees in the floral nectary a valuable phyletic character giving further support to the view that Monocotyledons have been derived from Dicotyledons through such forms as the Polycarpicæ. Finally, in a study of the development of *Butomus umbellatus*, Holmgren (35) draws attention to the frequent formation of several-celled archesporia in this species, and notes similar formations in the Ranunculaceæ. He does not insist too strongly upon the point, however, as many-celled archesporia are found in widely different plants.

Although the majority of botanists have now been led to regard Dicotyledons as representing the primitive stock—or at least to take up a non-committal attitude—one or two writers still believe, on anatomical grounds, that Monocotyledons are the more primitive and themselves gave rise to Dicotyledons by the splitting of the one original and primitive cotyledon. One of the chief supporters of this theory is Lyon (44, 45, 46) whose work on *Nelumbium* convinced him that in this form the development of two cotyledons may be traced through the division of a single terminal member, homologous with the single seed-leaf of Monocotyledons, which are to be derived directly from a primitive monocotyledonous Angiosperm stock. In order to account for the terminal position of this cotyledon, he suggests that it is not a phyllome, but an organ *sui generis*, comparable with the foot of Vascular Cryptogams, or with the sucker in *Gnetum* or *Welwitschia*. Lyon's theory of the primitiveness of Monocotyledons and their production of a dicotylar race need not be considered further, for it has not received any consistent explanation, nor are the anatomical (and other) differences between the two classes accounted for (cf. Sargant, 62, p. 175).

It may be safely concluded that on the whole, opinion at present inclines strongly towards the view that Monocotyledons have been derived from a dicotyledonous stock—a view suggested by Strasburger (69, pp. 317, 318) as long ago as 1872. Miss Sargant (57-62) has been largely responsible for the advancement of the theory,[2] and the work of other botanists, along similar or different lines from those followed by Miss Sargant, has contributed to its support.

---

[1] Stuchlik (70) gives a long list of references on the subject of Botanical Serology.

[2] Cf. Moss (51, p. 207).

IV. THE PROBABLE MANNER OF EVOLUTION OF THE MONOCOTYLEDONS FROM A DICOTYLEDONOUS STOCK.

If it is agreed that Monocotyledons have evolved from a dicotyledonous ancestry, a further problem presents itself, concerning the *manner* of their evolution from the parent stock, and the *cause* of their breaking away from it. Here again, considerable difference of opinion is encountered, and in this case, the differences appear to be increasing rather than decreasing.

The main issue depends upon the solution of the problem with regard to the derivation of the condition of monocotyly from the condition of dicotyly.

As Lotsy (42, p. 624) points out, there are various means by which this may have been accomplished, and these may be grouped under the headings of Syncotyly and Heterocotyly. It is proposed to treat these two processes separately giving as far as possible their probable causes.

1. **Syncotyly.** Syncotyly—or the fusion of the two cotyledons to form one member—has its chief exponent in Miss Sargant (57-62), whose anatomical investigations have convinced her that the vascular symmetry of monocotyledonous seedlings may be directly or indirectly referred to the same type as that of dicotyledonous seedlings in which fusion of the cotyledons has plainly taken place. Before proceeding to a special consideration of syncotyly, it may be well, perhaps, briefly to summarise Miss Sargant's conception of the Primitive Angiosperm from which she derives Monocotyledons. This author accepts Arber and Parkin's idea of the evolution of the Angiosperms (2 and 3), and derives both Monocotyledons and Dicotyledons from a race of primitive Angiosperms which she would place below the Ranalean plexus in Arber and Parkin's table (see 2, p. 77). Primitive Angiosperms possessed characteristics common to both the modern sub-groups: namely, secondary growth by means of a cambium; flowers of Ranalean type, Arber and Parkin's idea of the evolution of the angiospermous flower being accepted (2, figs 1, 2 and 4); closed carpels; endosperm; two cotyledons; and seedlings with tetrach vascular symmetry.[1] Primitive Angiosperm having two cotyledons, it is necessary to find a means of determining how the descendants along one line might come to possess only one. It is almost impossible to determine this from a study of the development of the young embryo within

---

[1] For views on the primitiveness (or otherwise) of tetrarchy see Tansley and Thomas (72), Thomas (73), Compton (10), Hill and de Fraine (34); see also Tansley's criticism of Miss Sargant's theory (71).

the embryo-sac. The case of such psuedomonocotyledons as *Ranunculus Ficaria*,[1] *Corydalis cava* and *Carum Bulbocastanum* illustrates this point. Resort is therefore made to the evidence of comparative seedling anatomy.

Very generally, in the seed-leaf of Monocotyledons, a true midrib is replaced by two equal bundles. In some forms these bundles are so arranged as to suggest that each represents the midrib of an ancestral cotyledon, and a comparison of certain monocotyledonous seedlings, such as *Anemarrhena*, with those of some Ranalean forms (for example, *Eranthis hiemalis*) supports this suggestion (58, p. 109; Pl. II). The *Anemarrhena* seedling anatomy may be taken as a primitive type, since it leads by intermediate forms through at least four lines within the Liliaceæ. It may be described shortly as follows (57, 58, p. 109; Pl. II, figs 1-6):—

The cotyledon of an *Anemarrhena* seedling is somewhat flattened, and the plumule is rather late in development. In the example figured by Miss Sargant, it is still completely enclosed within the base of the cotyledon. The axis, which is somewhat thickened immediately below the plumule, passes at once into the strongly developed primary root. The vascular system of this seedling is symmetrical, two large bundles running the whole length of the cotyledon, which is elliptical in transverse section. Towards the base of the cotyledon, the two bundles are slightly displaced from their hitherto symmetrical position by the formation and growth of the plumule; but although this displacement extends into the transition region, the transition itself takes place in a symmetrical manner. Three branches of protoxylem are derived from each xylem group, and each phloem group divides into two. The lateral branches of protoxylem fuse in pairs, and the result is a tetrarch root-stele.

In certain Dicotyledons, the seed-leaves are normally united to a greater or less degree, sometimes by one margin only, but more often by both. In the latter case the united petioles form a tube, sometimes of considerable length (see Sargant, 59; Table I, pp. 73, 74). Petiolar tubes of this kind are found in a good many of the Ranunculaceæ and in other orders; and in all investigated cases, they are accompanied by a much shortened and thickened hypocotyl.

---

[1] In this species the evidence from embryogeny has led Sterckx (66) to assume that monocotyly has arisen by fusion of two cotyledons; Hegelmaier (29) and Schmid (63), on the contrary, think that suppression of one cotyledon has taken place

The anatomical structure of the petiolar tube and thickened hypocotyl of *Eranthis hiemalis*—one of the Ranunculaceæ—recalls that of an *Anemarrhena* seedling. In the *Eranthis* seedling figured by Miss Sargant (58, Pl. II, figs. 7-12), the blades of the cotyledons alone are separate, the petioles being united throughout their whole length to form a slender cylinder. This cylinder is solid just below the blades and above the stem-bud, but hollow between these levels, and hollow again over the tuber on which the stem-bud is developed. Three bundles from each cotyledonary blade enter the cylinder, but the two lateral traces from each blade rapidly unite with their own midrib, so that the petiolar cylinder contains two bundles each representing a separate cotyledon. The section passing through the stem-bud shows each bundle dividing into two, and finally there are formed in the hypocotyl four bundles of stem-type, arranged more or less in pairs. As these bundles become more widely separated with the increasing girth of the hypocotyl, three, and ultimately four xylem groups are formed, corresponding to each pair of phloem groups. As the hypocotyl narrows again towards its base, the xylem collects into four masses, and the four phloem groups fuse in pairs. A diarch root-stele is formed by the disappearance of two of the protoxylem groups.

In spite of the differences in detail, the resemblances between *Anemarrhena* and *Eranthis* are sufficiently clear to suggest that each may be referred to the same dicotyledonous plan.

Zygadenus elegans, a species belonging to the same family as *Anemarrhena*—Liliaceæ—has seedlings exhibiting unilateral vascular symmetry, with one cotyledonary bundle. This type may be connected with the *Anemarrhena* type, however, by intermediate forms; and Miss Sargant finds that seedlings from other monocotyledonous families may be derived from a Liliaceous type, or shown to be similarly bisymmetrical.

In these bisymmetrical cases, fusion of the two original cotyledons may be supposed to have taken place by both margins, as clearly indicated in the case of *Eranthis* and other Dicotyledons, where a cotyledonary tube is formed. Miss Sargant further states that monocotyly may arise by fusion of the cotyledonary petioles by one margin only. She quotes the cases of *Ranunculus Ficaria*[1] and *Anemone apennina*,[2] conceiving these to be well-proved cases of the normal fusion of cotyledons by one margin only, and adds that fusions are not infrequently found in abnormal specimens of types having distinct cotyledons (59, p. 75), such as *Ranunculus repens*, *Ranunculus chius* and *Urtica dioica*. These instances suggest that the single seed-leaf of some other species of pseudomonocotyledonous Dicotyledons may have been formed in a similar way (see Sargant, 59, Table II, p. 76, 77),[1] and, of course, indicate the possibility of a similar origin of monocotyly in true Monocotyledons.

---

[1] Cf. the view of Hegelmaier (29) and of Schmid (63), that monocotyly in this species is due to suppression of a cotyledon. Compton (11, p. 802) thinks that "on the whole the tendency of the evidence seems to be in favour of the view that the seed-leaf of *R. Ficaria* represents a single cotyledon."

[2] Compton (11, p. 802) thinks there is some doubt about this species.

Miss Sargant next considers the apparently terminal position of the single cotyledon in Monocotyledons, maintaining that if it "be derived from the two cotyledons of an ancestor, it cannot really be terminal, but must represent the congenital fusion of two lateral members" (60, p. 339). In the case of *Delphinium nudicaule* (60, p. 339, figs. 1 and 2), which possesses a cotyledonary tube, the first leaf breaks through the tube near its base, and for some time appears as though laterally inserted on the cotyledonary axis. But as the leafy stem develops, the cotyledons are pushed aside and assume their true position as lateral organs. In the case of congenitally united cotyledons, a lateral position of the stem-bud is necessary to free development. The cotyledons are usually formed some time before the growing point of the stem, and naturally, the single rudiment which represents both cotyledons tends to lie in a straight line with the suspensor and future axis. Thus, when later the plumule is developed, it must take up a lateral position (see 60; p. 340, fig. 3, *Alisma*), and only attains its true terminal position after germination, when it pushes the cotyledonary member aside. *Tamus* (60, fig. 6) and *Commelina*, however, are examples in which the growing point is terminal and the cotyledon lateral from the first. *Corydalis cava* has a single cotyledon like that of *Tamus* in form and position (60, cf. figs. 4 and 5 with fig. 6); and the simplest explanation of both cases is that the single cotyledon represents "the fusion of two ancestral cotyledons, but that on account of the early formation of the rudimentary plumule, or perhaps because the cotyledons have united by one margin only . . . . the stem-bud has never lost its terminal position" (60, p. 340).

This view of the monocotyledonous embryo overcomes the difficulties of regarding the single cotyledon as a terminal leaf, or as in the case of *Nelumbium*, according to Lyon, as an organ of an entirely different nature.

Miss Sargant's next point in her very complete and consistent theory, is a consideration of the causes and advantages of cotyledonary fusion. The large number of Dicotyledons exhibiting cotyledonary fusion indicates that it does offer advantages under certain conditions.

---

[1] Cf. Compton (11, p. 803, footnote 3).

What these conditions are is indicated at once by the fact that cotyledonary fusion is accompanied in practically all cases by shortened and thickened hypocotyls[1] (as in *Eranthis*), and by the formation of underground storage organs of some kind. The plants possessing these characteristics are geophytes, that is, plants whose aerial organs persist for a short annual season only, the underground parts forming a storage of food materials through the dead season (cf. Areschoug, 4, p. 1). The fact that most Dicotyledons exhibiting cotyledonary tubes are highly specialised geophytes suggests that fusion of the cotyledons is an adaptation to this habit. A consideration of the conditions under which a typical geophyte lives—for example, in Arctic regions, or on Alpine summits—makes it evident that its seedlings must be exceptionally well-adapted to their environment in order to survive. By the end of the short period of growth the young seedling must be in a condition which will enable it to live during the adverse weather following; so that at the commencement of the vegetation season it begins at once to form its underground organs.[2] "In all cases however, the production of assimilating surfaces seems to be an object of secondary importance" and "concresent cotyledons may be regarded as an adaptation for producing effective assimilating surfaces with the least possible expenditure of material. The production of a single cotyledon, whether by the more complete fusion of two or in any other way, is also an economy as compared with the formation of two cotyledons" (59, p. 80).

After a consideration of the above facts, Miss Sargant concludes that Monocotyledons have evolved through adaptation to a geophilous habit, an indication as to how this may have taken place being given by certain geophilous Dicotyledons which possess a single cotyledonary member. Many of the distinguishing features between Monocotyledons and true Dicotyledons may be explained as having arisen as a result of such adaptation; for example, the presence of endosperm in the seed of most Monocotyledons is a character of highly specialised geophytes; the distribution of vascular bundles in the stem and the loss of cambium in Monocotyledons may be ascribed to the shortening and thickening of the axis; the disappearance of the primary root and development of an annual crop of adventitious roots are clearly connected with the annual recurrence of a period of vegetative activity; the form and venation of monocotyledonous leaves are the most suitable for insertion on the shortened axis and also for pushing up through the soil. The absence of a true epidermis on the root above the root-sheath[1] and the trimerous symmetry of the flower in Monocotyledons are points less easy of explanation, but in most respects, Miss Sargant's theory is exceedingly well supported and shows that there is much to be said for the origin of Monocotyledons from a dicotyledonous race by Syncotyly, certain Liliaceæ being considered to give the key to the situation.[2]

---

[1] The correlation of cotyledonary tubes and thickened hypocotyls has been noted by Sterckx (66, pp. 80, 81), Lord Avebury (Lubbock, 43, II, pp. 23, 24) and Darwin (13, p. 97).

[2] The behaviour of geophilous seedlings during the first season of growth falls into four classes:—

- i. The whole structure may remain underground—*Megarrhiza californica* and *Arum maculatum*.
- ii. The cotyledons only appear above ground—*Eranthis hiemalis* and *Fritillaria imperialis*. This is the most usual behaviour.
- iii. The cotyledons may remain underground in the seed, and the first leaf break through the soil—*Anemone nemorosa* and *Eucomis nana*.
- iv. Both cotyledons and foliage leaves come up above ground and act as assimilating organs—*Delphinium nudicaule*.

Compton (11, p. 800) from a study of teratological syncotyls amongst Dicotyledons, concludes that leaving the Spadicifloræ out of the question, syncotyly may well account for the origin of monocotyly in other Monocotydons.[3] He adds the following valuable observations to those of Miss Sargant:—With very few exceptions (*Serratula radiata*, *Limnanthes Douglasii*, *Cardamine* spp. and possibly *Megarrhiza californica* (cf. Sargant 59, p. 83), species forming a cotyledonary tube have albuminous seeds, so that the small and usually straight embryo develops in a homogeneous medium, the endosperm. If syncotyly occurred at all, it would be expected to be symmetrical under these conditions—that is, to affect both edges of the cotyledons equally. On the other hand, species which are normally dicotyledonous but which occasionally produce syncotyls, are mostly exalbuminous, the exceptions being about one in six. Amongst Monocotyledons, the Helobieæ are exalbuminous, and the embryos of this group possess unilateral symmetry, suggesting that syncotyly has taken place along one edge of the cotyledonary petioles. Assuming, as Compton does, the primitiveness of the Helobieæ, it seems as if unilateral symmetry must be primitive for Monocotyledons, rather than the Liliaceous bilateral symmetry, according to Miss Sargant. The alternative is to suppose, with Lotsy (see Diagram IV), that the Helobieæ and Liliifloræ are two independent lines from a common stock; the first line may have adopted asymmetrical syncotyly, having originated in an ancestor with exalbuminous seeds, while the second, descending from an albuminous type, became symmetrically syncotylous.

---

[1] Cf. Henslow (31, p. 732). This author ascribes the absence of an epidermis to the degenerating influence of a moist or aquatic habit.

[2] With regard to the primitiveness of the Liliaceæ, see also Lindinger (40), Lotsy (42), Hallier (28). Miss Sargant believes that aquatic Monocotyledons, such as the Helobieæ, may be explained as having taken to an aquatic habitat in order to escape competition with the better-equipped Dicotyledons on land; their characters must be regarded as secondary rather than primitive. Bessey, Wettstein and Warming, on the other hand, consider the apocarpous Helobieæ to be the most primitive of Monocotyledons, a view indicated by Hallier in 1905 (27); Lotsy also admits the claims of the group to primitiveness, deriving them from Pro-ranalean ancestors in common with the Liliifloræ. Nicotra (52) holds that the Cyclanthaceæ are the primitive Monocotyledons.

[3] In this connection, it is interesting to note that Mottier (50) concludes, from his work on anomalous Dicotyledons, that the facts of their embryology "throw little or no light upon the relative antiquity of the two classes of Angiosperms" (p. 460).

2. **Heterocotyly.** Heterocotyly, according to Lotsy (42, p. 624), may be of different kinds. Firstly, there may be a division of labour between the cotyledons, one remaining in the seed and becoming a suctorial organ, and the other escaping and forming the first assimilatory organ.

This view is well illustrated by certain geophilous species of *Peperomia* described by A. W. Hill in 1906 (32; figs. 1-9, p. 420). In this genus a series may be traced from species which are truly dicotyledonous—for example, *Peperomia pellucida*—to species in which there is a monocotyledonous club-shaped absorbing organ, from which all trace of its original leaf-like character has disappeared, as in *Peperomia parviflora*. *Peperomia peruviana* is an intermediate stage, both cotyledons having a distinctly leaf-like form, but one remaining within the seed and forming an absorbing organ, the other becoming the first aerial assimilating organ.

According to Hill, the cotyledon of some of the Araceæ and *Tamus communis* is closely comparable with the absorbing cotyledon in *Peperomia*, and their first leaf with the aerial organ of that form. He believes that monocotyly arose by division of labour between the cotyledons on account of adaptation to a geophilous habit, and the consequent necessity for an efficient absorbing organ within the seed. Its efficiency would be helped by the removal of all other embryonic structures from the seed as soon as possible after germination; consequently the rudimentary assimilating cotyledon, the plumule and radicle are carried down into the ground. Thus in course of time, one cotyledon may have become developed so as "to form a pseudo-terminal absorbent organ (Text-fig. 7, p. 420), while the other cotyledon—the apparently lateral 'first-leaf'—is left to develop from its rudiment outside the seed (cf. Text-figs. 8 and 9, p. 420)" (32, p. 422). Indeed, as Lotsy's subdivisions of heterocotyly suggest, this series may end in monocotyledonous cases, where the second aerial cotyledon is completely disguised as the first leaf (42, p. 624).

Further, Hill thinks it is possible that the median bundle of the single seed-leaf of some Monocotyledons has become divided in more advanced types, such as *Anemarrhena* (considered by Miss Sargant to be primitive), this being correlated with the parallel venation of the leaves of the Liliaceæ (32, p. 423). In opposition to Miss Sargant, he considers the type of anatomy in an *Arum* seedling as being more primitive and near dicotyledonous ancestors (such as Piperaceæ), and the *Anemarrhena* type as derived through such simpler Liliaceous forms as *Zygadenus*.

Lotsy is in complete agreement with Hill in regarding the Spadicifloræ as an example of heterocotyly. As may be seen from his phylogenetic scheme (Diagram IV), he derives them from ancestors near the Piperales. Compton also apparently agrees with this view (11, p. 801)[1].

The second kind of heterocotyly is that in which reduction or even complete suppression of one cotyledon has taken place.

Lotsy quotes as an example of reduction of one cotyledon the embryo of grasses, in which the scutellum functions as an ordinary suctorial cotyledon, while the epiblast is considered as representing the reduced second cotyledon. This view was put forward by Mirbel in 1810 (49, p. 424 in note), and some twenty years later, as we have seen, Agardh (1, p. 197) held that Grasses were the only true Monocotyledons because one cotyledon had become completely suppressed. As Compton points out in his recent paper (11, p. 800), it is unsafe to theorise about this case, for there still exists too great diversity of opinion as to the morphology of the grass embryo.

The chief supporter of the suppression theory is Henslow (30, 31), whose papers in 1892 and 1911 bring forward evidence, partly from experiments on land and water plants, in support of his contention which may be stated briefly as follows:—Monocotyledons and Dicotyledons come from a common dicotyledonous stock, members of which gave rise to true Dicotyledons or to Monocotyledons according to their habitat on land or by, or in, water. The forms subjected to an aquatic or moist habitat became degenerate[1] owing to the weakening effect of water by saturating the protoplasm. This is shown in the case of division and fenestration of leaves of aquatic plants, loss of secondary growth by means of a cambium, and in the case of Monocotyledons, by complete loss of one cotyledon. Henslow maintains—apparently in answer to Miss Sargant's criticism that there is no evidence of suppression—that the second strand in the cotyledon of that author's so-called primitive Monocotyledons, is the last relic of the cotyledon which has been otherwise totally arrested (31, p. 743). After the aquatic Angiosperms had been subjected to weakening conditions through many generations, the effect of such conditions became fixed and hereditary, so that at the present time, Monocotyledons are unable to adapt themselves completely to land conditions in competition with the Dicotyledons—hence the retention of an aquatic habit by so many of them.[2]

---

[1] From a study of the morphology of germination, Gatin (24, p. 54) concludes that there is not sufficient evidence for the adoption or rejection of Hill's theory.

In support of heterocotyly, Compton (11, p. 802) quotes the case of *Ranunculus Ficaria*. It will be remembered that according to Miss Sargant (59, p. 75), this is a case of asymmetrical syncotyly, or union of the cotyledonary petioles by one edge only (see also Sterckx, 66, p. 42). But according to Compton, the balance of evidence—such as vascular anatomy and venation of the cotyledonary blades—is in favour of the view of Hegelmaier (29) and Schmid (63, p. 211) that the seed-leaf in *Ranunculus Ficaria* is a single organ. The evidence applies to *Corydalis* spp., *Carum Bulbocastanum*, *Pinguicula* spp., *Abronia* spp. Compton concludes that in these cases it is difficult to decide whether complete suppression of one cotyledon accounts for heterocotyly, or whether the missing cotyledon has been retarded in development, and now appears as the first foliage leaf.

Lotsy (42, p. 624) broad-mindedly admits the origin of monocotyly in any of the ways described by various writers. He thinks, however, that the case of syncotyly is less well-established than that of heterocotyly.[3]

---

[1] Cf. de Vries (16, p. 15), who insists on the degenerate nature of Monocotyledons.

[2] A comparison of Henslow's view of the origin of Monocotyledons with that of Miss Sargant, shows that, according to Henslow, the aquatic habitat is primarily the *cause* of the evolution of Monocotyledons; while according to Miss Sargant, it is largely the *result* of the development of a monocotyledonous condition.

[3] Guillaumin (25, p. 232) also admits that monocotyly may have arisen by fusion of two cotyledons, or by suppression of one.

V. CONCLUSION.

From the foregoing review it will be seen that there is very great diversity of opinion concerning the cause and manner of development of the Monotyledons, while their immediate ancestry, though generally thought to be dicotyledonous, is still a matter for discussion. The speculations for which Arber and Parkin (2, 3) have been largely responsible, concerning their more remote ancestry, have little more than a theoretical value.[1] They are intensely interesting, and are within the bounds of possibility, but in the present state of our knowledge, they are somewhat daring. The gap between Gymnosperms and Angiosperms is still waiting to be filled by discoveries as important as those of Pteridosperms and Bennettitales.

---

[1] See Oliver (53); Scott (64, p. 658); Lignier (38); Coulter and Chamberlain (12, p. 280)

BOTANY SCHOOL,
CAMBRIDGE. *March, 1914.*

LIST OF REFERENCES.

1. Agardh, C. A. "Lärobok i Botanik." Pt. I. Malmö, 1829-32.
2. Arber, E. A. N., and Parkin, J. "On the Origin of Angiosperms." Journ. Linn. Soc., Bot., Vol. 38, 1907, p. 29.
3. Arber, E. A. N., and Parkin, J. "Studies in the Evolution of the Angiosperms: the Relationship of the Angiosperms to the Gnetales." Ann. of Bot., Vol. 22, 1908, p. 489.
4. Areschoug, F. W. C. "Beiträge zur Biologie der geophilen Pflanzen." Lund, 1896.
5. Bailey, I. W. "The Relation of the Leaf-trace to the Formation of Compound Rays in the Lower Dicotyledons." Ann. of Bot., Vol. 25, 1911, p. 225.
6. Bessey, C. E. "The point of divergence of Monocotyledons and Dicotyledons." Bot. Gaz., Vol. 22, 1896, p. 229.
7. ,, "Phylogeny and Taxonomy of the Angiosperms." Bot. Gaz., Vol. 24, 1897, p. 145.
8. Brongniart, A. "Énumération des Genres de Plantes cultivés au Muséum d'Histoire Naturelle de Paris." Paris, 1843.
9. Campbell, D. H. "Lectures on the Evolution of Plants." London, 1899.
10. Compton, R. H. "An Investigation of Seedling Structure in the Leguminosæ." Journ. Linn. Soc., Bot., Vol. 41, 1912, p. 1.
11. ,, "An Anatomical Study of Syncotyly and Schizocotyly." Ann. of Bot., Vol. 27, 1913, p. 793.
12. Coulter, J. M., and Chamberlain, C. J. "Morphology of Angiosperms." 1903 and 1910.

13. Darwin, C. "The Power of Movement in Plants." London, 1880.

14. De Candolle, A. P. "Théorie élémentaire de la Botanique." (Ed ii), Paris, 1819.

15. De Jussien, A. L. "Genera Plantarum secundum Ordines Naturales disposita." Paris, 1789.

16. De Vries, H. "Species and Varieties, their Origin by Mutation." Chicago, 1905.

17. Drude, O. "Die Systematische und Geographische Anordnung der Phanerogamen," in Schenk's Handbuch der Botanik, III, 2, 1887, p. 175.

18. Eames, A. J. "On the Origin of the Herbaceous Type in Angiosperms." Ann. of Bot., Vol. 25, 1911, p. 215.

19. Endlicher, S. "Genera Plantarum secundum Ordines Naturales disposita." 1836–1840.

20. Engler, A., und Prantl, K. "Pflanzenfamilien—Nachtrag und Register zu Teil II—IV." Liepzig, 1897.

21. Engler A. (with E. Gilg). "Syllabus der Pflanzenfamilien" (7th ed.). Berlin, 1912.

22. Fries, R. E. "Ein unbeachtet gebliebenes Monokotyledonenmerkmale bei einigen Polycarpicæ." Ber. der deutsch. bot. Ges., Bd. 29, 1911, p. 292.

23. Fritsch, K. "Die Stellung der Monokotylen im Pflanzensystem." Engler's Bot. Jahrb., Bd. 34, Beibl. Nr. 79, 1905, p. 22.

24. Gatin, C. L. "La Morphologie de la Germination, et ses rapports avec la Phylogenie." Rev. Gén. de Bot., t. 21, 1909, p. 147.

25. Guillaumin, A. "Remarques anatomiques sur la Syncotylie et la Monocotylie de quelques plantules de Dicotylédones." Rev. Gén. de Bot., t. 24, 1912, p. 225.

26. Hallier H. "Ueber die Morphogenie, Phylogenie und den Generationswechsel der Achsenpflanzen (Vorläufige Mittheilung)." Ber. der deutsch. bot. Ges., Bd. 20, 1902, p. 476.

27. ,, "Provisional Scheme of the Natural (Phylogenetic) System of Flowering Plants." NEW PHYTOLOGIST, Vol. 4, 1905, p. 151.

28. ,, "Système phyletique des Angiosperms." Archives Néerlandaises, 1911–1912.

29. Hegelmaier, F. "Vergleichende Untersuchungen über Entwickelung dikotyledoner Keime." Stuttgart, 1878.

30. Henslow, G. "A Theoretical Origin of Endogens from Exogens by Self-Adaptation to an Aquatic Habit." Journ. Linn. Soc., Bot., Vol. 29, 1892, p. 485.

31. ,, "The Origin of Monocotyledons from Dicotyledons through Self-Adaptation to a Moist or Aquatic Habit." Ann. of Bot., Vol. 25, 1911, p. 717.

32. Hill, A. W. "Morphology and Seedling Structure of the Geophilous Species of *Peperomia*, together with some Views on the Origin of Monocotyledons." Ann. of Bot., Vol. 20, 1906, p. 395.

33. Hill, T. G. "On the Seedling Structure of Certain Piperales." Ann. of Bot., Vol. 20, 1906, p. 161.

34. ,, and de Fraine, E. "A Consideration of the Facts Relating to the Structure of Seedlings." Ann. of Bot., Vol. 27, 1913, p. 257.

35. Holmgren, I. "Zur Entwicklungsgeschichte von *Butomus umbellatus* L." Svensk Botanisk Tidskrift, Bd. 7, 1913, p. 58.

36. Horwood, A. R. "The Past History of Monocotyledons, with Remarks on Their Origin." Scottish Bot. Review, Vol. 1, 1912, pp. 164 and 216.
37. Kny, L. "Die Entwickelung der Parkeriaceen dargestellt an *Ceratopteris thalictroides* Brongn." Nova Acta der Ksl. Leop.-Carol. Deutsch. Akad. der Naturf., Bd. 37, Nr. 4, 1875.
38. Lignier, O. "Essai sur l'Évolution morphologique du règne végétale." C. R. Assoc. Fr. Av. Sci., 1908.
39. Lindinger, L. "Die Struktur von *Aloë dichotoma* L., mit anschliessenden allgemeinen Betrachtungen." Beih. z. Bot. Centralbl., Bd. 24, Abt. I, 1909, p. 211.
40. ,, "Bemerkungen zur Phylogenie der Monokotylen." Naturwissen. Wochenschr., N.F., Bd. 9, Nr. 5, 1910.
41. Linnaeus, C. "Philosophia Botanica." Stockholm, 1751.
42. Lotsy, J. P. "Vorträge über botanische Stammesgeschichte. III, i. Cormophyta-Siphonogamia." Jena, 1911.
43. Lubbock, Sir J. "A Contribution to our Knowledge of Seedlings. Vols. i and ii." London, 1892.
44. Lyon, H. L. "Embryogeny of *Nelumbo*." Minnesota Bot. Studies, Vol. 2, 1901, p. 643.
45. ,, "The Phylogeny of the Cotyledon." Postelsia, 1901, p. 57.
46. ,, "The Embryo of the Angiosperms." American Naturalist, Vol. 39, 1905, p. 13.
47. Maneval, W. E. "The Development of *Magnolia* and *Liriodendron*, including a Discussion of the Primitiveness of the Magnoliaceæ." Bot. Gaz., Vol. 57, 1914, p. 1.
48. Mez, C., und Gohlke, K. "Physiologisch-Systematische Untersuchungen über die Verwandtschaften der Angiospermen." Beiträge zur Biol. der Pfl., Bd. 12, 1913, p. 155.
49. Mirbel, C. F. B. "Examen de la division des végétaux en Endorhizes et Exorhizes." Ann. du Muséum, XVI, 1810.
50. Mottier, D. M. "The Embryology of Some Anomalous Dicotyledons." Ann. of Bot., Vol. 19, 1905, p. 447.
51. Moss, C. E. "Modern Systems of Classification of the Angiosperms." NEW PHYTOLOGIST, Vol. 11, 1912, p. 206.
52. Nicotra, L. "Sur le Système des Monocotyledonées," Oesterr. bot. Zeitschr., Bd. 60, 1910.
53. Oliver, F. W. "Pteridosperms and Angiosperms." NEW PHYTOLOGIST, Vol. 5, 1906, p. 232.
54. Porsch, O. "Die Abstammung der Monokotylen und die Blütennektarien." Ber. d. deutsch. bot. Ges., Bd. 31, 1914, p. 580.
55. Ray, J. "Historia Plantarum." London, 1686–1704.
56. Rendle, A. B. "The Classification of Flowering Plants. Vol. 1." London, 1904.
57. Sargant, E. "A New Type of Transition from Stem to Root in the Vascular System of Seedlings." Ann. of Bot., Vol. 14, 1900, p. 633.
58. ,, "The Origin of the Seed-leaf in Monocotyledons." NEW PHYTOLOGIST, Vol. 1, 1902, p. 107.
59. ,, "A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings." Ann. of Bot., Vol. 17, 1903, p. 1.
60. ,, "The Evolution of Monocotyledons." Bot. Gaz., Vol. 37, 1904, p. 325.
61. ,, "The Early History of Angiosperms." Bot. Gaz., Vol. 39, 1905, p. 420.
62. ,, "The Reconstruction of a Race of Primitive Angiosperms." Ann. of Bot., Vol. 22, 1908, p. 121.

63. Schmid, B. "Beiträge zur Embryo-Entwickelung einiger Dicotylen." Bot. Zeit., Vol. 60, 1902, p. 207.

64. Scott, D. H. "Studies in Fossil Botany." 2nd Ed., London, 1909.

65. Seward, A. C. "Notes on the Geological History of Monocotyledons." Ann. of Bot., Vol. 10, 1896, p. 205.

66. Sterckx, R. "Recherches anatomiques sur l' embryon et les plantules dans la famille des Rénonculacées." Mém. de la Soc. Roy. d. Sci. de Liège, Sér. 3, t. 2, 1899.

67. Stopes, M. C., and Fujii, K. "Studies on the Structure and Affinities of Cretaceous Plants." (Abstract from the Proceedings of the Royal Society, 1909). Ann. of Bot., Vol. 24, 1910, p. 231.

68. Stopes, M. C. "Further Observations on the Fossil Flower, *Cretovarium*." Ann. of Bot., Vol. 24, 1910, p. 679.

69. Strasburger, E. "Die Coniferen und die Gnetaceen." Jena, 1872.

70. Stuchlik, J. "Serologie *v.* Botanice." Biologickélisty, roč. 2, 1913.

71. Tansley, A. G. "'Reduction' in Descent." New Phytologist, Vol. 1, 1902, p. 131.

72. ,, and Thomas, E. N. "The Phylogenetic Value of the Vascular Structure of Spermophytic Hypocotyls." Report of Brit. Assoc., Sect. K, 1906, p. 761.

73. Thomas, E. N. "A Theory of the Double Leaf-Trace Founded on Seedling-Structure." New Phytologist., Vol. 6, 1907, p. 77.

74. Warming, E. "Fröplanterne (Spermatofyter)." Copenhagen and Christiania, 1912.

75. Wettstein, R. R. von. "Handbuch der Systematischen Botanik." Leipzig and Vienna, 1911.

APPENDIX.

Since the above review was written three important papers dealing with the origin of Monocotyledons have appeared.

The first of these is concerned with the point of contact between the Monocotyledons and the Dicotyledons. Nitzschke (3) maintains that, owing to its position, the embryo-sac is less likely to become affected by external (ecological and physiological) conditions than other plant organs. He accordingly has investigated and compared the developmental history of the embryo-sacs of the apocarpous nymphæaceæ—*Cabomba* and *Brasenia*—and those of certain forms of the Helobieæ, particularly of Butomaceæ and Alismataceæ. He finds that of all Ranalean types investigated by him or by other authors, the apocarpous nymphæaceæ show the greatest similarity, so far as embryo-sac development is concerned, to the Helobieæ. His conclusion is, therefore, that they may have been derived from a common ancestor.

The other two papers deal with the origin of the monocotyledonous condition.

Miss Farrell (2), working on the ovary and embryo of *Cyrtanthus sanguineus*, concludes that the sheath of monocotyledons is probably the result of fusion of two or more cotyledons. In this species, the youngest observed stages of the embryo, show the stem-tip surrounded by a four-lobed sheath; the growth of this sheath (1, p. 516) produces the cotyledonary ring in which the four lobes or growing points persist for a time, but ultimately grow together in pairs producing two cotyledonary rudiments. Finally the cells of one of the cotyledons cease to divide, and an apparently single terminal cotyledon results. Miss Farrell considers her investigation to furnish a last proof of the theory of the derivation of monocotyly from dicotyly.

The work of Coulter and Land (1) on *Agapanthus umbellatus* is in agreement with that of Miss Farrell with regard to the origin of the cotyledonary sheath. Their observations form the basis of a new theory of the origin of monocotyly. *Agapanthus umbellatus* may produce monocotyledonous or dicotyledonous embryos, and in either case, the cotyledons arise as lateral structures from a peripheral zone surrounding the stem-apex of the proembryo. The proembro is massive, a condition which Coulter and Land consider to be primitive for Angiosperms, and at its broad, somewhat flattened shoot-end the meristemic activity of the peripheral cells produces the cotyledonary zone, in which two or more growing points appear. By continued growth of the whole zone a sheath is formed surrounding the depressed stem-apex, and equal growth of the two primordia produces a dicotyledonous embryo. In other cases, however, only one growing-point continues to divide, so that apparently only one cotyledon is developed. Coulter and Land maintain that, since the sheath and the cotyledons are all one structure, the production of a so-called single cotyledon is due to the "growth of the whole cotyledonary zone under the guidance of a single growing point" (1, p. 515), instead of the distribution of activity between two separate primordia. In polycotyly, more than two primordia appear and persist in growth. The authors compare the zonal development of the cotyledonary sheath with its varying number of growing points, with the zonal development of sympetalous corollas, which according to them, provides a parallel case.

In view of the importance attached by Miss Sargant and other workers to the vascular anatomy of seedlings, it may be noted that Coulter and Land consider the vascular strands to be secondary structures, the position and appearance of which are determined by the position of the growing points. They cannot therefore be regarded as phylogenetically important structures.

BOTANY SCHOOL,
CAMBRIDGE. *August 1914.*

LIST OF REFERENCES.

1. Coulter, J. M., and Land, W. J. G. "The Origin of Monocotyledony." Bot. Gaz., Vol. 57, 1914, p. 509.
2. Farrell, M. E., "The Ovary and Embryo of *Cyrtanthus sanguineus*." Bot. Gaz., Vol. 57, 1914, p. 428.
3. Nitzschke, J. "Beiträge zur Phylogenie der Monokotylen, gegründet auf der Embryosackentwicklung apokarper nymphæaceen und Helobien." Cohn's Beiträge zur Biologie der Pflanzen Bd. 7, 1914, p. 223.

MORPHOLOGICAL AND BIOLOGICAL NOTES ON NEW AND LITTLE-KNOWN WEST-HIMALAYAN LIVERWORTS. II.

BY SHIV RAM KASHYAP, B.A., M.Sc.,
Professor of Botany, Government College, Lahore.

[WITH EIGHT FIGURES IN THE TEXT.]

IT was shown in the last paper[1] that *Targionia*, and not *Exormotheca*, must be taken to be the simplest type of the Compositæ. The bearing of some new Himalayan liverworts on the dorsal position of the female carpocephalum will be discussed in the present paper.

---

[1] NEW PHYTOLOGIST, Vol. 13, pp. 206-226.

EXORMOTHECA TUBERIFERA KASHYAP.

Solms-Laubach[1] has investigated the structure of *Exormotheca pustulosa*, but several new points were made out in the species described below.

The plants were found growing singly on dry and exposed eastern slopes. They are two or three times dichotomously branched with long linear lobes and closely attached to the soil. The lobes are up to 10 mm. long and up to, but usually much less than, 2 mm. broad (Fig. 1). The dorsal surface is green, has usually a deep narrow groove along the middle line and is covered with conspicuous stomata. The latter are raised above the general level of the thallus and are often confluent, two chambers opening by a single pore. The size of the stoma and the number of the cells surrounding the pore are very variable. The pore may be round or elongated and the cells surrounding it are not much different from the ordinary epidermal cells. The chambers are arranged in a single layer and are full of simple green filaments which reach nearly to the roof. The terminal cells of the filaments are elongated and tapering upwards and contain fewer chloroplasts than the lower cells (Fig. 2, *a*). In this respect the filaments resemble those of *Fegatella conica*,[2] but they are longer. Immediately below the floor of the chambers there is one layer of large cells and below them are the small cells of the thick midrib which strongly projects downwards. The purple ventral surface bears two rows of purple lunate overlapping scales obliquely directed forwards and outwards. The scales are occasionally hyaline. They arise from the midrib and have an entire margin (Fig. 2, *c*). There is no trace of any filamentous appendage as has been described in other species of the genus. In one specimen a scale was observed with a filament

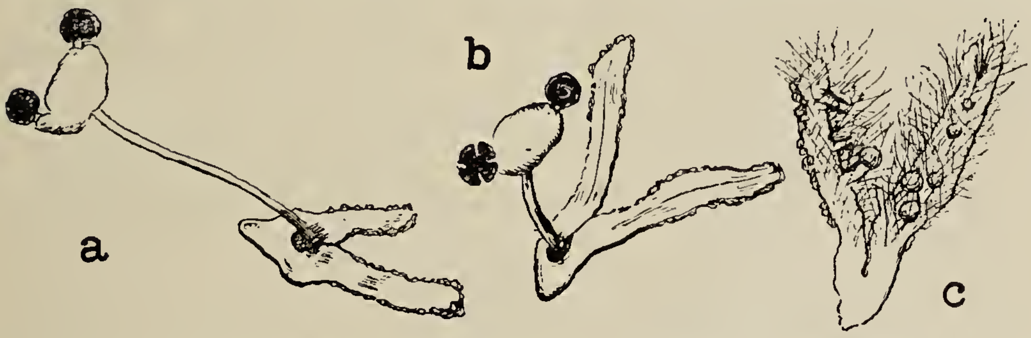


FIG. 1. *Exormotheca tuberifera*: *a*, *b*, plants with ripe sporogonia, × 3; *c*, a plant seen from below showing tubers, × 3.

---

[1] Bot. Zeitung, Bd. 55, 1897.

[2] Cavers, "On the structure and biology of *Fegatella conica*," Ann. Bot., vol. 18, 1904, p. 90, Pl. VI, Fig. 11; "Inter-relationships of the Bryophyta," Fig. 25 (p. 45 of Reprint).

two-celled at the base, arising out of the middle of the surface. Nor any trace of mucilage cells was ever found. The scales project from the margin only slightly and do not bend over the dorsal surface. Their cells do not contain chloroplasts.

The plant is remarkable on account of the formation of tubers. At the end of the vegetative season the apex of the plant becomes gradually narrowed, the dorsal assimilating tissue also decreases gradually. Ultimately we have a short thick cylindrical structure which is directed downwards, and is more or less buried in the soil and protected by the scales. The growing point in this way survives and continues its growth next year. This is the reason why, in the vegetative season, all plants of the species which form more or less definite tubers by the thickening of the apex, and are marked by the letters B and C in the list given in the last paper,[1] have a thick base. This is the case with the present species, *Stephensoniella brevipedunculata*, *Athalamia pinguis*, *Gollaniella pusilla*, *Cyathodium tuberosum* and *Cryptomitrium himalayensis* among others. More definite tubers are formed in this species by the modification of ventral shoots (Fig. 1, *c*). Each tuber has a short cylindrical stalk and is a spherical body, about 0·5 mm. in diameter, covered with rhizoids. At one place on the tuber there is a small depression in which is situated the growing point which is covered with minute purple scales. The apical cell in the growing point cuts off segments very regularly on the sides. How many other cutting faces it has was not determined. The rest of the tuber is surrounded by a single layer of cells which have lost their contents, while the cells in the interior are full of starch.

Exormotheca tuberifera is monœcious. The antheridia occur often in a depression in one group behind the female receptacle or along the midrib in the median groove. If fertilisation fails to occur in any of the archegonia of the female receptacle, which is situated in the angle between two shoots, the latter begin to form antheridia in the median groove. They are formed in two zigzag rows. When mature, each antheridium fills the cavity of the chamber in which it lies, leaving no space between its large hyaline wall-cells and the wall of the chamber. The chamber opens above by a papilla which has often a red colour. A young antheridium is shown in Fig 2, *d*, where the sequence of walls shows that the development is probably not different from that of the other Marchantiales.

---

[1] New Phytologist, vol. 13, 1914, p. 208.

The female receptacle is situated in a pit in the angle between two vegetative shoots. This pit has no anterior margin but laterally and posteriorly the walls bend inwards and more or less cover the young receptacle. If no archegonium is fertilised the receptacle remains merely as a hemispherical cushion and does not develop further, while the two shoots begin to form antheridia. If the archegonia are fertilised the two shoots still go on growing but do not produce any antheridia. The archegonia are one to four in each lateral group accompanied by a few simple filaments (paraphyses) of about four cells each. The small receptacle tissue contains air-chambers filled with green filaments, but very few or no chloroplasts are found in the cells of the septa separating the

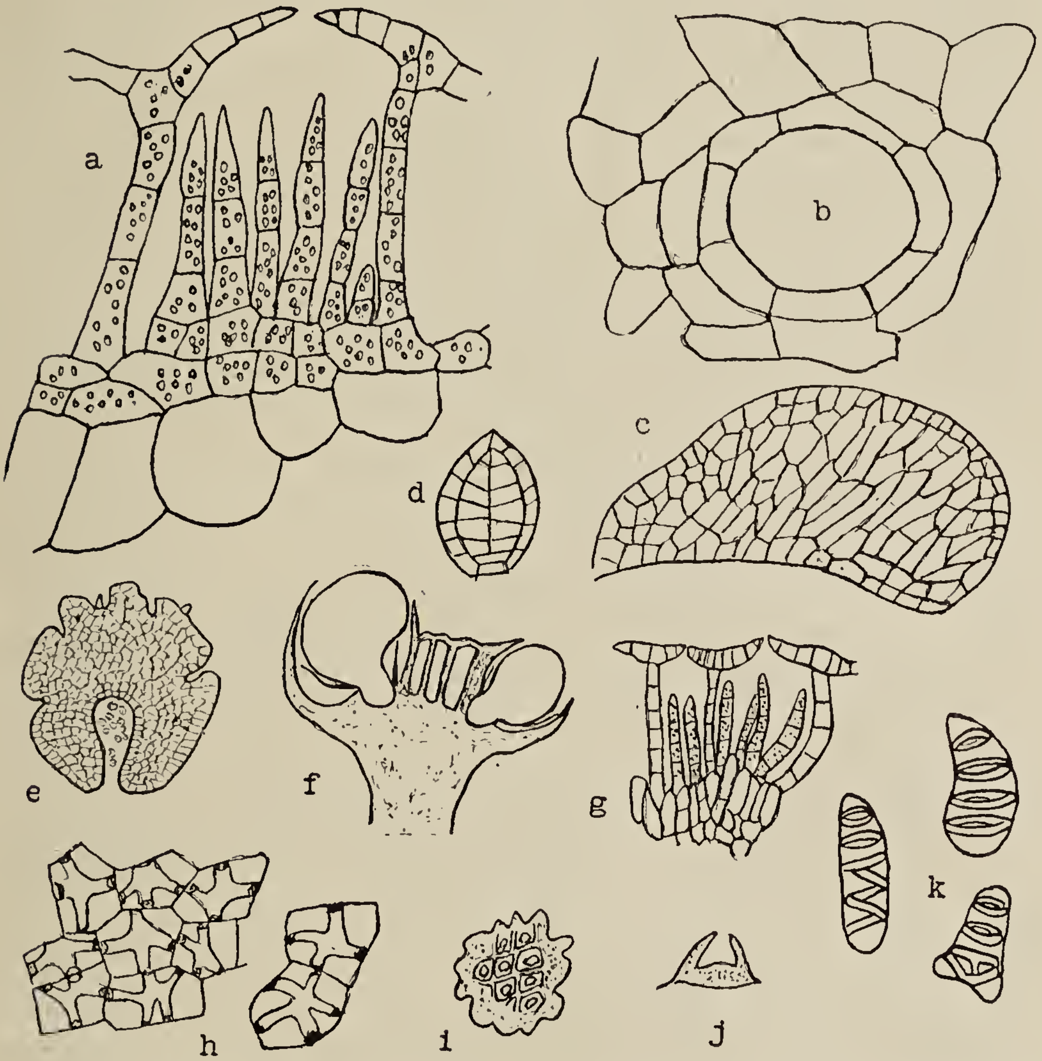


FIG. 2. *Exormotheca tuberifera*: *a*, part of longitudinal section of thallus, showing structure of air-chamber, × 200; *b*, stoma from carpocephalum, seen from above, × 200; *c*, ventral scale, × 50; *d*, young antheridium, × 50; *e*, transverse section of stalk of carpocephalum, × 50; *f*, vertical section of carpocephalum (assimilating filaments in air-chambers not shown), × 15; *g*, part of *f*, showing filaments in air-chambers, × 50; *h*, a few cells of the capsule wall, seen from within, × 200; *i*, spore, × 200; *j*, papillæ of spore cut vertically, × 400; *k*, clater-like cells from apex of capsule, × 200.

chambers and in the cells forming the roof. Solms-Laubach has stated that there are no stomata on the female receptacle of *E. pustulosa.* Stephani[1] also states that the chambers on the female receptacle do not open to the outside. Stomata, however, are found on the female receptacle of the present species and they are bounded by more definite cells both as regards the number and the size of the latter. Here the stoma is surrounded by a single ring of about seven cells and is not much raised (Fig. 2, *b*, *f*, *g*). The mature receptacle is usuallycarried upwards on a long stalk but occasionally the stalk remains very small. The stalk has a deep furrow containing rhizoids (Fig. 2, *e*).One or both involucres may develop sporogonia. The latter may be one or two in each involucre. The capsule has a small foot but a long seta. The latter may be as much as 1·5 mm. in length. The capsule is always fully exserted and directed upwards (Fig. 5, *a*, *b*). The involucre is at first bilabiate but later on opens by a circular mouth. The thin calyptra is left behind in the involucre.

The capsule-wall is thickened in the same way as described by Solms-Laubach for *E. pustulosa.* The bands on the cells forming the lid are thicker and broader than those on the other cells. Sometimes in this region the radial walls of a few cells here and there are uniformly thickened in addition to their possessing the ordinary bands. In the upper half of the capsule four or five bands start from the centre of the inner wall and pass on to all the radial walls (Fig. 2, *h*). In the lower half of the capsule wall the bands are simply U-shaped. The elaters are 120 to 140μ long with three or four lax spiral bands. The spores (Fig. 2, *i*, *j*) are tetrahedral, 55 to 60μ in diameter, covered with many hollow high conical papillæ on the convex surface. The operculum has on its inner surface a few short elater-like cells which are spirally or annularly thickened. Sometimes these thick bands anastomose irregularly (Fig. 2, *k*). Dehiscence of the capsule takes place by four irregular valves.

The plant differs from the other species of this genus so far described in the following respects. (1) The scales have no appendages; (2) the plants form apical and particularly ventral tubers; (3) the female receptacle has stomata.

STEPHENSONIELLA BREVIPEDUNCULATA KASHYAP.

The plants are found either singly growing hidden among grass and moss plants, or aggregated in large patches on bare rocks in more or less exposed places. Each plant has a thick base indicating that growth has been continued from the apical tuber of the last year's growth. It is either simple or dichotomously branched once or twice, and is closely attached to the substratum. The lobes are obovate with a cordate apex (Fig. 3, *a* to *d*). The plants are light green in colour, spongy above but having a thick midrib projecting downwards. The upper surface is areolated, each areole corresponding to a chamber below. The chambers (Fig. 4, *a*) which occur in a single layer are very large, directed obliquely forwards and have no assimilating filaments in them. Each dorsal areole has a stoma in it which may open into a single chamber or into two to four chambers. The septa separating these chambers are seen just below the stoma. The stoma is thus of a typical confluent form, and when four chambers open by a common pore the latter has a peculiar cruciform appearance. Each pore is surrounded by one or two rings of hyaline cells (Fig. 4, *b*). The number of these cells is variable, and often the cells of the inner ring are more or less collapsed to form a thin membrane projecting into the opening of the stoma. The ventral surface is greenish and has both kinds of rhizoids. The scales (Fig. 4, *c*, *d*) are hyaline, small and in two rows. They arise from the midrib but do not reach the margins. Each scale has a few filamentous appendages arising from the apex and the margin. In the young state the cells of the scale contain chloroplasts.

---

[1] "Species Hepaticarum," vol. 1, 1900, p. 218.

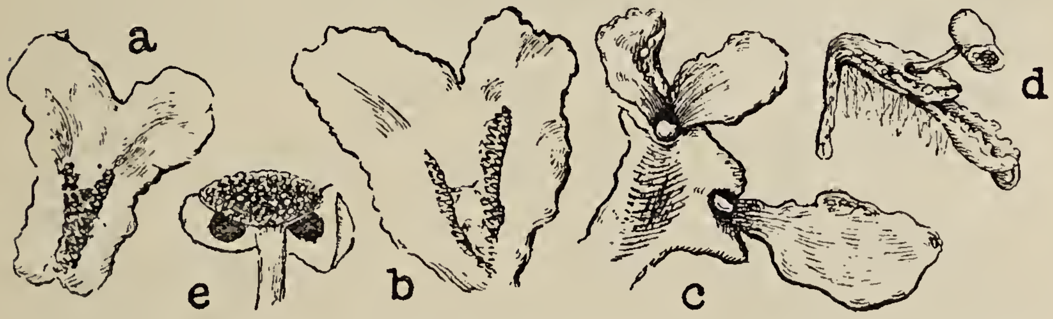


FIG. 3. *Stephensoniella brevipedunculata:* *a*, *b*, male plants, × 6 ; *c*, unfertilised female plant ; *d*, female plant with ripe sporogonia (the peduncle should be a little shorter), × 5 ; *e*, carpocephalum with two ripe sporogonia, × 4.

The plants form thick adventitious ventral shoots occasionally, but every branch which lives up to the end of the vegetative season forms an apical tuber. At this time the growing point ceases to form wings and produces in this way a small cylindrical downwardly directed tuber covered with scales. This tuber has no chambers and its cells are full of starch grains. The growing point survives buried in the earth and continues its growth next year. The rest of the plant dies at the end of the season.

The plants are diœcious. The male plants are found in very small numbers, consequently very few female plants produce ripe sporogonia. The antheridia are formed in a broad median dorsal groove in large numbers. They arise close to each other in two or four zigzag rows and form a definite receptacle. In the mature state the red papillæ of the chambers in which they are formed are very conspicuous. The antheridial receptacle does not, however, stop the growth of the plant, which continues to form vegetative tissue after the formation of antheridia has ceased. The receptacle may fork as the thallus forks (Fig. 3, *a*, *b*). No paraphyses are met with among the papillæ, and usually no vegetative tissue is formed between them excepting the separating septa. Occasionally, however, the male receptacle forks, even though the thallus does not show any signs of forking, and the two branches of the receptacle, after growing for some time independently, again come close to each other and meet, leaving a small island of assimilating tissue. The structure of the mature antheridium is like that of *Exormotheca tuberifera*, though very few plants were collected in which the antheridia had not discharged their contents. The apex of the male plants ultimately forms a tuber.

The female plants were found in large numbers, but mostly unfertilised. The female receptacle is always terminal. It arises as a small hemispherical cushion in a deep pit whose anterior wall is wanting. Laterally and posteriorly the pit is overhung by the vegetative tissue which bends inwards and protects the young receptacle. The receptacle in this respect resembles that of *Exormotheca*. It is also protected in the young state by the scales whose filamentous appendages bend over the anterior depression and are in intimate contact with the receptacles. The receptacle has two lateral groups of archegonia in two grooves as is the case in *Exormotheca*. The archegonia are one to six in each group. Posteriorly, the receptacle has a large number of paraphyses which are simple filaments of four or five cells each. Laterally also the archegonia have a few similar paraphyses near them. Thus the young receptacle, in addition to being protected by the cup-like depression, is also protected by the filaments on all sides. Soon, however, while the receptacle is still quite young, the growth of the thallus is continued forwards. This is invariably the case with all female plants, and the receptacle thus soon becomes dorsal instead of being terminal. As the apex grows after the formation of the female receptacle it may form a tuber at once and so form only a small amount of tissue. Or it may grow out into a large shoot (Fig. 3, *c*, *d*) which may remain simple or may divide. Again, sometimes, the adventitious shoot divides very soon and very near the old apex, so that it seems as if the main shoot itself had forked, but there is a groove between the new shoot and the wings of the old shoot.

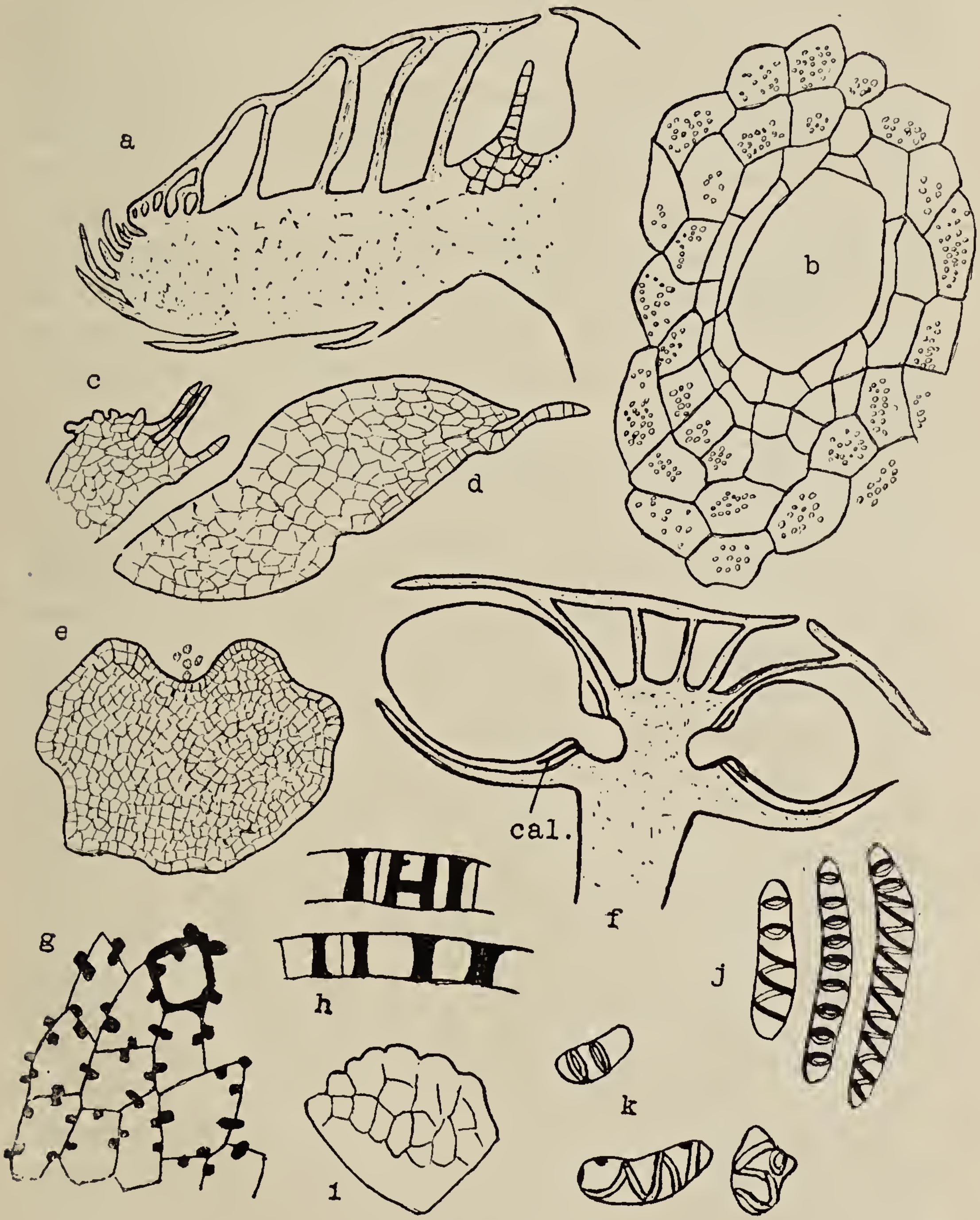


FIG. 4. *Stephensoniella brevipedunculata*: *a*, longitudinal section of thallus × 50; *b*, stoma seen from above, × 200; *c*, *d*, ventral scales, × 50; *e*, transverse section of carpocephalum stalk (peduncle), × 50; *f*, vertical section of carpocephalum with two ripe sporogonia (cf. Fig. 3, *e*), × 20; *cal.*=calyptra; *g*, part of capsule wall in surface view, × 200; *h*, parts of capsule wall in longitudinal section × 200; *i*, spore, × 200; *j*, elaters, × 200; *k*, elater-like cells from apex of capsule, × 200.

The archegonia, as stated above, are one to six in each group and have rather long necks with about fifteen cells in each row. They are at first directed upwards but later on become horizontal. The tissue of the receptacle contains large air-chambers without any assimilating filaments, but opening by pores similar to those on the thallus. If the archegonia are not fertilised the receptacle remains very small (Fig. 3, *c*) as is also the case in *Exormotheca.* If one or more archegonia are fertilised it becomes large and is raised on a very short peduncle. The latter is only 0·75 to 1·5 mm. long and has a shallow groove anteriorly (Fig. 4, *e*) which contains a few tuberculate rhizoids. The latter may not even reach the base. In the meantime an involucre is developed on each side round the young sporogonia, two of which may ripen in one involucre. The involucre is tubular, opening by a wide mouth (Fig. 3, *e*), and has very thin hyaline walls consisting of a single layer of cells near the margin. There are no scales either at the base or the apex of the peduncle.

The sporogonium is perfectly horizontal and is wholly or partially included. It has a small foot and a very small seta (Fig. 4, *f*). Dehiscence of the capsule takes place by three or four valves irregularly. The cells of the capsule wall which consists of a single layer of cells have thick brown bands on their radial walls only (Fig. 4, *g*, *h*) and the inner and outer walls are always thin. Occasionally a cell here and there near the apex has all its radial walls uniformly thickened. There is never the appearance of radiating bands on the inner wall as is found in *Exormotheca.* The apex of the capsule has on its inner surface a few very short elater-like cells which are only annularly or spirally thickened and are simpler than the similar cells of *Exormotheca* (Fig. 4, *k*). The spores are tetrahedral and large, 80 to 100μ in diameter, opaque and covered densely with low large and small papillæ irregularly toothed (Fig. 4, *i*). The elaters are very small, only 80 to 140μ in length with only annular bands or a single lax spiral band (Fig. 4, *j*).

In some specimens two small projecting tuberous processes were found under an involucre in which none of the archegonia were fertilised. They are, no doubt, rudimentary adventitious shoots which are so common in this plant.

It will be seen from the above description that the plant must be placed near *Exormotheca.* It is undoubtedly a reduced form derived from that genus, as is shown by the decrease in the thickening of the cell-walls of the capsule-wall and the elaters and the continuation of growth after the formation of the female receptacle. It resembles *Exormotheca* in the position of the male and female receptacles, the number and position of the involucres in the carpocephalum, and to a certain extent the structure of the sporogonium. The latter, however, is much simpler in *Stephensoniella*, as is shown by the thickening on the wall-cells of the capsule and the elaters. *Stephensoniella* differs from the genus *Exormotheca* in its simpler sporogonium, empty air-chambers and, above all, in the continuation of growth after the formation of the female receptacle. This last feature coupled with the simple sporogonium is extremely interesting as it points out the way in which forms like *Corsinia* and *Boschia* have originated. Indeed, *Stephensoniella* is a connecting link between *Exormotheca* on the one hand and *Corsinia* and *Boschia* on the other. Its resemblance to the latter is seen in several features. The male receptacle in the two is similar. Secondly, the female receptacle of *Boschia* may be derived from *Stephensoniella* by supposing that the dichotomy of the primary female branch does not take place and it may be compared to the condition found in *Targionia*. The structure of the capsule wall and the elaters is very much alike in *Boschia* and *Stephensoniella*. Of course, it is not meant that *Boschia* has descended directly from *Stephensoniella* by suppression of the dichotomy but it must have descended from some similar ancestor. Similarly, *Corsinia*, though further reduced, must have come from some similar ancestor with a large number of involucres. It has been mentioned that the involucres of *Stephensoniella* are only formed if the archegonia are fertilised. Similarly the protecting scale of *Corsinia* only develops after fertilisation. If only a single sporogonium is produced it remains simple, equivalent to a single involucre; but if several sporogonia are produced it becomes lobed, that is, equivalent to several involucres.

The origin of forms like *Riccia* may be considered here. Unfortunately there is no great evidence on which one may decide the question. Goebel's view that *Riccia* may be derived from forms like *Targionia*, which he would put in the Simplices, seems to be very probable. The chief fact bearing on the question is the arrangement of the archegonia in some of the Ricciaceæ in median dorsal rows. This condition would be reached if the apical growing point of a form like *Targionia*, instead of being displaced downwards, were to go on growing forwards, along with the total reduction of the involucre. It must be noted, however, that there is a great gap between *Riccia* and *Targionia* as regards the structure of both the gametophyte and the sporophyte generations.

When Goebel[1] suggested a wholesale reduction in the Marchantiales he added that his conclusions are only probable and take for granted many transitional forms which are nowadays very rarely found in the vegetable kingdom. Fortunately we do find a few such transitional forms in these days so far as the Marchantiales are concerned. Two such forms have already been described: (1) *Aitchisoniella* which connects *Exormotheca* and *Targionia*; (2) *Stephensoniella* which connects *Exormotheca, Boschia* and *Corsinia.* Another such form will be described below under *Plagiochasma articulatum.* Thus though the general conclusion of Goebel has been strongly confirmed his division of the Marchantiaceæ into Simplices (containing *Targionia* and *Cyathodium*) and the Compositæ cannot be maintained.

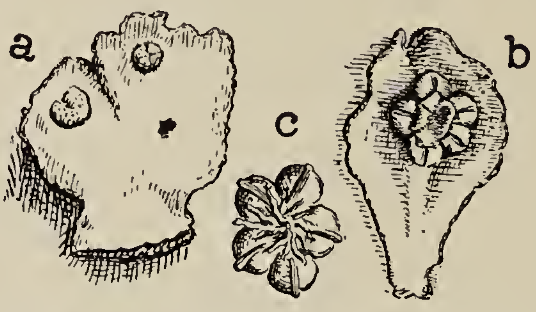


FIG. 5. *Plagiochasma appendiculatum: a,* thallus with a male (left) and a female receptacle (right), × 2; *b,* lobe with a ripe carpocephalum, × 2; *c,* carpocephalum from below, × 2.

PLAGIOCHASMA APPENDICULATUM L. ET L.

This species has been met with in various parts of northern India, both in the Himalayas and the Plains, according to Stephani.[2] The plant which I propose to discuss under this name, however, differs in several respects from the description given by Stephani and the peculiar features are noted below.

The size and general form and appearance of the thallus are just as Stephani describes them, but the thallus and the tissue of the female receptacle contain a few brown oil-cells. Sometimes these cells occur only in the receptacle. Each stoma is bounded by three series of eight cells each. The scales which bear large hyaline appendages, one or two to each scale, do not reach beyond the margins but only half way to them, though the appendages are conspicuous at the anterior depression where they bend over the growing point and cover it. The thallus sometimes bears apical adventitious shoots. The male receptacle is usually horse-shoe shaped having two growing points (Fig. 5, *a*). Sometimes the

[1] Flora, Bd. 101, pp. 43-97, 1910.

[2] "Species Hepaticarum," vol. 1, 1900, p. 79.

growing points again show signs of forking. The receptacle has ordinary simple pores between the antheridial papillæ, like those of the thallus but the female receptacle, which is slightly concave on the dorsal side when mature, has a well-developed assimilating tissue with barrel-shaped pores (Fig. 6, *b*). The most important feature of the plant, however, is that the receptacle is not two- or three-lobed as described by Stephani, but may have as many as nine lobes. Five or six involucres in one receptacle are most commonly met with (Fig. 5, *b*). Two or three carpocephala may arise, one after the other, on the dorsal side of the thallus. Similarly three antheridial receptacles may be formed, one after the other, on a separate lobe of the thallus which has no carpocephalum, or a carpocephalum may be formed in front of the male receptacle. An interesting feature in connection with the female receptacle is the "æstivation" of the valves of the involucre. The valves are folded in a peculiar manner in the present species, *P. articulatum*, to be described next, and another species (*P. Aytonia*), three species which were examined. The margins of the young involucre are bent inwards at first, but as the capsule increases in size, they are pushed to one side (Fig. 6, *a*) so that they press against the inner surface of the wall of one of the valves. Later on one margin becomes perfectly free while the other remains permanently folded along the inner surface. The process is illustrated in the accompanying

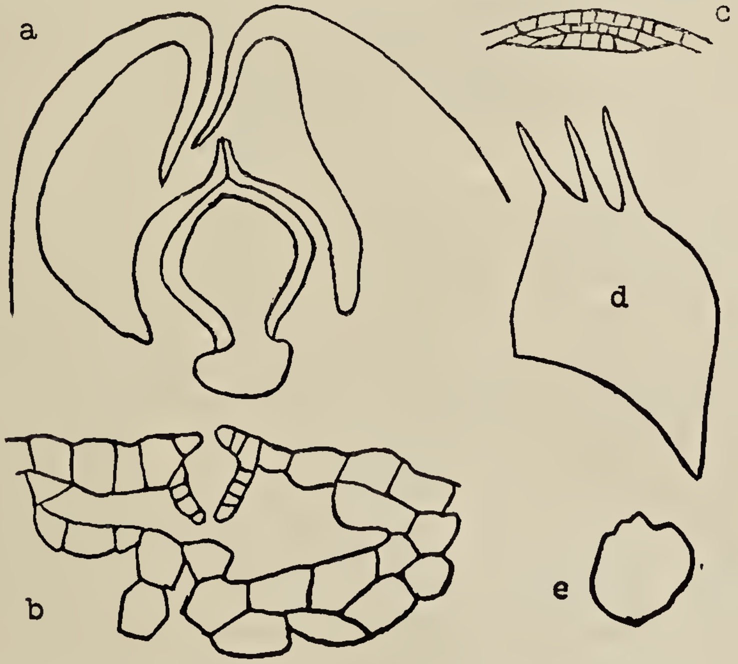


FIG. 6. *Plagiochasma appendiculatum* (*a*, *b*, *c*) and *P. articulatum* (*d*, *e*): *a*, horizontal section of involucre, × 50; *b*, stoma from female receptacle, × 200; *c*, vertical section of operculum, × 200; *d*, ventral scale, × 15; *e*, transverse section of peduncle, × 15.

diagrams (Fig. 7). In *Reboulia hemispherica* the margins are similarly bent inwards at first but later they become perfectly free and are pushed outwards. It would be interesting to know if this is a constant feature of the genus *Plagiochasma*. The writer has examined only the above-mentioned three species and every involucre examined has shown this arrangement of the involucre margins. When the number of involucres is large, as in *P. appendiculatum*, the free margin usually belongs to the same side of the several involucres. In one case, when the receptacle had nine involucres, all with ripe sporogonia, eight of them had the free margin on the same side; the ninth had the free margin on the other side, so that here the two free margins belonging to the adjacent involucres were close to each other, while in the rest the free and folded margins alternated with each other.

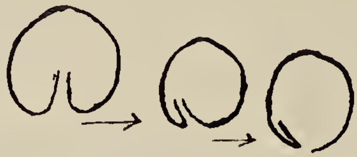


FIG. 7. Diagrams (transverse sections) to illustrate the "æstivation" of the involucre in *Plagiochasma*; for description see Text.

The lid (operculum) of the capsule is three cells in thickness and these cells are equally thickened on all sides (Fig. 6, *c*). Sometimes, when the plants occur in dry exposed places, the capsule becomes dry very early and the elaters remain without any spiral bands though they have thick brown walls. This condition of the elaters is met with much more often in *P. articulatum*. The size of the spores and elaters as given by Stephani is 51μ and 250μ respectively. The writer found that the spores and elaters in one capsule were often 60μ and 220μ respectively. This relation between the size of the spores and elaters is found in other species also, e.g., *Targionia hypophylla*, an increase in the size of the spores being accompanied by a decrease in the size of the elaters.

PLAGIOCHASMA ARTICULATUM KASHYAP.

This species was often found growing along with *P. appendiculatum*, and forms along with the latter one of the commonest thallose liverworts in Mussoorie. It also occurs, however, in exposed and dry places where the latter cannot live. A few plants of both species are found in winter, about December and January, on the river bank in Lahore also, but they never produce any fruit here. They probably arise from the spores brought down by the water from the hills.

The plant is decidedly more xerophilous than *P. appendiculatum*, and is also smaller and thinner. It is repeatedly forked and may be up to 2·5 cm. in length and 8 mm. in breadth. The lobes are oblong-obovate, dark green above with conspicuous stomata, and purple below. Each stoma has three series of cells surrounding it with seven or eight cells in each series. The purple scales (Fig. 6, *d*) are overlapping, similar to those of *Reboulia hemispherica*,[1] and each has two or three long narrow purple appendages which bend over the growing point. The scales do not reach more than half way to the margins. The vegetative thallus and the tissue of the female receptacle contain numerous brown oil-cells. They are specially numerous in the latter where they occur among the epidermal cells. The thallus produces ventral adventitious shoots.

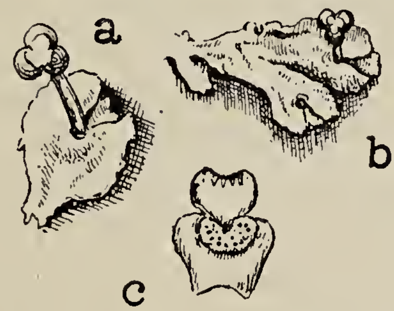


Fig. 8. *Plagiochasma articulatum*: *a*, *b*, plants with carpocephala, *a* × 2, *b* × 1; *c*, lobe with male receptacle, × 2.

P. articulatum is monœcious. The antheridial receptacles may be formed one after another, or an antheridial receptacle may be followed by a female receptacle. The antheridial receptacle is a horse-shoe shaped structure surrounded by small scales as in *P. appendiculatum* with two growing points. The female receptacle is also similar to that of the last-mentioned species but it has never more than four involucres, usually it has only one to three (Fig. 8). The dorsal surface of the female receptacle is slightly concave but it has the barrel-shaped pores as is the case also with *P. appendiculatum*. The pores on the male receptacle are simple. *Plagiochasma*, therefore, lags behind *Reboulia* in this respect among others, that the male receptacle has simple pores in *Plagiochasma*, but the pores are barrel-shaped in *Reboulia*.[2] The æstivation of the involucre has already been described. The spores are closely reticulate, lamellate, 60 to 80μ in diameter. The elaters are normally bispiral, 220 to 260μ in length.

[1] Cavers, "Inter-relationships of the Bryophyta," Fig. 20, *b*, *c* (p. 39 of Reprint).

[2] Cavers, "On *Reboulia hemispherica*," Naturalist, 1904; "Inter-relationships of the Bryophyta," 1911, Figs. 22, 23.

The most important feature of this plant, however, is that both the male and the female receptacles are terminal at first and not dorsal outgrowths as in other species of *Plagiochasma.* After the receptacles have been laid down growth stops for some time but is later continued by an adventitious apical shoot (Fig. 8). The plant in this respect behaves in the same way as *Preissia commutata.*[1] The plant has invariably a jointed appearance. The new adventitious shoot sometimes remains very small, hardly more than a small process. Usually, however, it grows for some time and produces a second receptacle. Even a third receptacle may be formed in this way. The stalk of the carpocephalum, which is about 3 mm. long, is more or less sulcate on all sides, but there is a deeper groove always on the anterior side though it has no rhizoids (Fig. 6, *e*). The base of the receptacle has only small scales.

It has been mentioned before that the stalk of the carpocephalum in *Stephensoniella brevipedunculata* is very small and has a very shallow groove containing only a few rhizoids. This condition is correlated with the continued forward growth of the thallus. In *P. articulatum* we have another stage of reduction where the rhizoids have been altogether suppressed and the forward growth begins even earlier than in *Stephensoniella* after the formation of the female receptacle. In other species of *Plagiochasma* there is never any stoppage of growth and the carpocephalum appears to be purely dorsal from the very beginning. Two other considerations point to the same conclusion. (1) In some of the higher Marchantiales, e.g., *Marchantia,* both the thallus and the receptacle possess barrel-like pores. In other genera, e.g., *Reboulia,* both the male and female receptacles have barrel-like pores while the thallus has ordinary simple pores.[2] In *Plagiochasma* only the female receptacle has barrel-shaped pores while the male receptacle and the thallus have simple pores. The barrel-shaped pores have persisted in the sexual receptacles while they have become reduced in the thallus to simple pores. (2) It is simpler to suppose that the scales surrounding the sexual receptacles of plants like *Plagiochasma* represent the ventral scales of a branch system than to suppose that they have arisen as such from the dorsal side which ordinarily does not possess them.

It will be seen from the above description of *P. articulatum* that the stalk of *Plagiochasma* is homologous with the stalk of the receptacle of the Compositæ and is not a structure which has arisen independently.

[1] Cavers, "Contributions to the biology of the Hepaticæ. Part I.—*Targionia, Reboulia, Preissia, Monoclea.*" Leeds and London, 1904.

[2] Cavers, "Inter-relationships of the Bryophyta," Figs. 21-23.

It appears, therefore, that the dorsal position of the sexual receptacle has appeared at various levels independently. Two such cases have been mentioned. (1) At the level of *Exormotheca*, *Stephensoniella* has diverged to one side and leads to forms like *Boschia* and *Corsinia.* (2) At the level of *Reboulia*, *Plagiochasma* has been given off. It may be supposed that *Corsinia* has arisen from some form like *Plagiochasma* owing to the similarity of the structure of the capsule wall, but the structure of the elaters and the highly organised sexual receptacles are against this view. Then, again, we know no transitional forms between the two genera. (3) *Monoselenium* presents a third case. (4) *Preissia commutata*, which still has a well-developed composite female receptacle with two rhizoid furrows in the carpocephalum stalk. These are the four important examples showing the origin of a dorsal carpocephalum. In the case of *Stephensoniella*, *Monoselenium*, and probably *Preissia*, the growing point produces several archegonia in succession, though in *Preissia* Stephani[1] states that the archegonia are transversely (and not at all longitudinally) inserted.[1] In *Plagiochasma*, and the Operculatæ and Astroporæ in general, the growing point produces usually a single archegonium though in some species of *Fimbriaria*,[2] *Santeria*[3] and *Peltolepis*[3] each involucre often contains more than the archegonium. In an undetermined species of *Fimbriaria* from Mussoorie the writer also found two sporogonia in one involucre in several cases, but in these cases it was clear that the intervening walls of two involucres lying side by side had not developed owing to the great proximity of the sporogonia, as a rudimentary septum was found between the two and the latter were also arranged transversely.

---

[1] Species Hepaticarum," p. 154. As shown by Leitgeb (" Untersuchungen über die Lebermoose," Heft. 6, p. 109) and by Cavers (" Contributions to the biology of the Hepaticæ," p. 32), the archegonia in each involucre in *Preissia* are developed in the same centripetal succession as in *Marchantia*. "The archegonia begin to arise before the branching of the young receptacle is completed ; each of the growing points undergoes division while the archegonia are being formed, and as the receptacle is growing out in four radiating lines, the archegonia become arranged in tangential rows " (Cavers, *loc. cit.*).

[2] Campbell, " Mosses and Ferns."

[3] Cavers, " Inter-relationships of the Bryophyta," p. 37.

LABORATORY NOTE.

DEMONSTRATION OF CILIA IN LIVING *VOLVOX.*

THE method described in the following note has been found useful and very satisfactory for the demonstration of moving cilia for class purposes, etc.

Úlehla[1] in his work on cilia by dark-ground methods, found that of the members of the Volvocaceæ which he tried, only *Pandorina* was suitable for observation; the body of *Volvox* shone too brightly when thus illuminated, to permit of the study of the cilia. He apparently used young colonies.

I have found that although the cilia are very difficult to see when the colonies are freely swimming, yet they can be strikingly exhibited by the method.

A Zeiss paraboloid is employed as a substage illuminator with an arc lamp, as source of light, to produce the dark-ground illumination; the condenser must be very carefully centred. Fully developed colonies of *Volvox* are taken, placed on the slide in a little water and covered with an unsupported cover slip, which may be pressed very lightly with a needle. This serves to keep the colonies still and of course also flattens them to a certain extent. The motion of the cilia may be slowed down a little by this treatment, but is by no means stopped. A good focus may now be obtained on the edge of the colony. The cilia are then very clearly seen as bright lines against the dull ground, even with low powers, with which when the whole colony is in the field, a complete fringe of cilia is often evident around the colony. The manner of movement of the cilia appears to be much as in *Pandorina*, but it is not easy to study this with high powers. The very regular rhythm of the ciliary motion[2] as a whole is strikingly seen, the movement appearing to run round the contour of the colony in waves.

The fact that the colony is held in position for any length of time, makes the object specially suitable for demonstration purposes. The activity ceases after a time, but other colonies on the same slide, which have not been subjected to the intense illumination, will often be found still to show the movement well.

THE BOTANY SCHOOL,
CAMBRIDGE.
S. REGINALD PRICE.

---

[1] Úlehla, V. "Ultramikroskopische Studien über Geisselbewegung." Biol. Centralbl., Bd. 31, 1911, p. 701.

[2] See, *e.g.*, Pfeffer, "Physiology of Plants," Eng. Trans., Vol. III, p. 269.

THE
NEW PHYTOLOGIST.

VOL. XIII, No. 10. DECEMBER, 1914.
[PUBLISHED DECEMBER 28TH, 1914.]

INTERNATIONAL PHYTOGEOGRAPHIC EXCURSION (I.P.E.) IN AMERICA, 1913.

(concluded).

MONTEREY AND CARMEL.

ON September 15th most of the party left San Francisco for Monterey and Carmel, where Dr. MacDougal, Director of the Tucson Desert Laboratory of the Carnegie Institution of Washington, took charge of the arrangements till practically the close of the tour at Tucson, Arizona, at the end of the month. Through Dr. Macdougal's efforts a large grant was obtained from the Carnegie Institution for hospitality to the international party, and by his forethought, his genius for organisation, and the unremitting pains, attention and kindness which he lavished on the needs, both physical and intellectual, of his guests, this portion of the tour formed a most brilliant close to a brilliantly successful excursion. To Dr. MacDougal and to all his willing lieutenants, most particularly Dr. Cannon, Mr. Sykes and Dr. Forrest Shreve, the whole party lies under the deepest debt of gratitude.

The Monterey-Carmel district is well-known as the home of a group of very local endemic species, of which the Monterey Pine (*Pinus radiata*) and the Monterey Cypress (*Cupressus macrocarpa*) are the most conspicuous. Forest of the Monterey Pine covers the low dry hills near the coast between Monterey and Carmel, with chaparral or dry grassland in the more open places. Magnificent groves of *Cupressus*, many of the trees tortured by the wind into the queerest shapes, occur on the shallow rocky soil at Cypress Point, forming the outermost fringe of the pinewoods. *Quercus agrifolia* is very frequent, scattered through the dry grassland. The landscape, especially between Carmel and Cypress Point, is very striking. The weird wind-forms of the trees, especially *Quercus agrifolia*—*Pinus radiata* seems to be almost unaffected by wind—and the colouring of the landscape in September produce an effect very strange to the eyes of a European, unless it be rivalled in parts of Spain. Brown, brown-green, and light orange predominate. *Usnea* thickly covers the dead branches and twigs on the windward side of the oaks and *Trentepohlia* forms a brick-red feltwork on the dead branches of the cypresses. In the rock-bound bays the enormous fronds of the giant Laminarian seaweeds rise and fall on the Pacific swell. The prevailing brown-yellow tone of the landscape was marvellously enhanced at sunset by a flood of orange light from the west.

SOUTHERN CALIFORNIA.

On the morning of September 17th the party left Carmel and travelled southwards on the Southern Pacific towards Los Angeles, passing through much characteristic Californian country—broad fertile valleys, and hills covered with chaparral alternating with the stretches of dry grassland and scattered evergreen oaks so often mentioned. On crossing the Santa Margarita mountains, a few miles before reaching San Luis Obispo, the party met with quite an exciting adventure. The train was held up for several hours just outside a tunnel, because the next tunnel was on fire. At dusk the word came that we were to be transferred to another train on the other side of the burning tunnel. We had to reach the other train by a narrow path over the chaparral-covered mountain, the chaparral having just been burnt by the fire so that the blackened soil was still hot. Encumbered with our "hand-luggage," almost more than we could carry for any distance, we struggled along the narrow path, and in the middle of the route met a line of people in the same case, coming from the other train, and "being transferred" to the one we had just left. The slope was steep and it was difficult to pass and keep one's footing. There were old infirm people, and women with babies and children. It took about an hour to perform the journey of less than a mile, and the scene, lighted up by the lamps and torches of the railway men and backed by the indescribably vivid orange of the Californian afterglow behind the hills, was unforgettable. Everyone was exceedingly kind and helpful, and the patient uncomplaining way in which those who suffered most took the unpleasant experience was exceedingly striking. As we passed the burning end of the tunnel the fierce flaming of the gigantic beams fallen from the roof across the opening was very impressive in the gathering night. The fire was so serious that after repeated and ineffectual efforts to put it out the tunnel had to be sealed, and the coast-line—the main route from San Francisco to Southern California—was completely blocked for about two months while the tunnel was repaired. Eventually we arrived at Santa Barbara in the middle of the night and stopped there instead of at Los Angeles as had been intended.

The morning of September 18th was spent at Santa Barbara, a beautiful place with lovely gardens full of sub-tropical flowers and humming birds. The old Spanish mission is absolutely a bit of Southern Europe transported to America, and very pleasant to the homesick European. The town is backed by chaparral-covered mountains, very Mediterranean in aspect. Los Angeles, the busy flourishing metropolis of southern California, was reached at night, and after dinner in the town, the night-train was taken to Mecca, where a stop was made to visit the Salton Sea.

THE SALTON SEA.

On the morning of September 19th we woke to find ourselves in desert, and that of a very arid type—with an average yearly rainfall of less than 3 inches and a maximum evaporation of 120 inches. After breakfast we drove from Mecca several miles across the desert to the edge of the Salton Sea, a lake formed in the bottom of a salty "sink" by the accidental inflowing of water from the Colorado river. The whole of this basin is considerably below sea-level. The flat desert supports an open shrub-vegetation consisting chiefly of *Prosopis* spp., *Larrea tridentata*, *Parosela* spp. and *Cercidium (Parkinsonia) torreyanum*. The lake itself has rapidly receded since the influx of water was stopped in 1907 and is still receding year by year owing to the high evaporation. The dead trees and shrubs are being exposed by the receding waters. On the emersed beaches plants rapidly spring up, and this vegetation gradually changes as the conditions become more arid. At first the beach-line is colonised by growths of *Typha latifolia*, *Scirpus americanus* and *Salix nigra*, the last-named growing to a considerable height. *Distichlis spicata*, *Spirostachys (Allenrolfea) occidentalis*, and *Atriplex* spp. soon appear on the salty soil, and are eventually replaced by the typical desert-vegetation, *Prosopis*, *Isocoma*, etc.[1]

In the afternoon we visited a fine date orchard at Mecca, where the finest strains of date palm from all parts of North Africa are tried. The date industry of this region is growing rapidly.

---

[1] For a very full account of the colonisation of the emersed beach lines see D. T. MacDougal, "The Salton Sea," Carnegie Institution of Washington, 1914. See Review, NEW PHYTOLOGIST, October, 1914, p. 280.

On this afternoon the highest air-temperature encountered on the tour was registered. In the Middle West we had more than once had temperatures of over 100°F., but at Mecca a thermometer showed 115°F. in the shade. On the shore of the Salton Sea, where the relative humidity is high for such temperatures, owing to the proximity of the great body of water, the heat was decidedly trying. In the date-orchard the screened thermometer registered 108°F. at 5.30 p.m.

TUCSON AND THE ARIZONA DESERT.

During the night of September 19th we continued our railway journey along the edge of Salton Sea and crossed the Colorado River into Arizona only seven miles from the Mexican frontier. In the morning we were travelling through the Arizona desert and approaching Tucson, and here we caught our first glimpse of that imposing plant *Carnegia gigantea (Cereus giganteus)*, which stands up here and there as a column 20 or 30 feet high in the midst of the desert scrub.

The whole of September 20th was spent at the famous Desert Laboratory two or three miles outside the town of Tucson, on the lower slopes of Tumamoc Hill. Here Dr. MacDougal and the staff of the Laboratory had spared no pains to make our visit as pleasant and profitable as might be during the short time available. The different members of the staff gave short informal accounts of the researches being conducted at the Laboratory, many of them of great interest and importance. Dr. Forrest Shreve gave us an instructive little talk on the climate of Tucson and its relation to the vegetation. Dr. Livingston gave a demonstration of his atmometer cups, now widely used throughout the United States.

This is not the place to give any account of the work carried on at the Desert Laboratory, which is fully dealt with in the annual reports issued by the Carnegie Institution and in the other publications emanating from this important centre of research. It is sufficient to say that Dr. MacDougal and his fellow-workers are continuously making determined attempts to penetrate to the more fundamental questions of desert ecology, and with a large measure of success.

The vegetation of the neighbourhood of Tucson is fairly familiar to ecologists from the papers of Dr. MacDougal, Dr. Spalding and other workers at the Desert Laboratory, and no good purpose would be served by attempting a necessarily superficial description of it here. The country may fairly be called "semi-desert," since it has a distinct summer rainfall period in addition to the winter period and is thus climatically different from "true" desert. Correspondingly the vegetation is more luxuriant and much more numerous in individuals than is the case in the typical North African deserts. It is the "dry bush steppe" of various Continental writers. The dominant growth-form is the fair-sized shrub, much bigger than the North African undershrubs, with small highly xerophilous and sometimes deciduous leaves. The leading species are *Larrea (Covillea) tridentata*, *Parkinsonia microphylla* and *Fouquieria splendens*. Here and there the branched columns of the giant cactus rise far above the scrub and, locally, species of *Opuntia* and *Echinocactus* occur in considerable numbers. Only in places do grasses or other herbs form anything like continuous ground cover. Along the channels and "washes" the mesquite *(Prosopis)* occurs abundantly and grows quite luxuriantly, together with species of *Populus*, *Salix* and *Fraxinus*.

SANTA CATALINA MOUNTAINS.

On the afternoon of September 21st the party motored across the desert to the foot of the Santa Catalina range, on which the next few days were to be spent. The evening meal—taken at a camp at the base of the mountains amid a grove of giant cacti (*Carnegia*)—was made quite luxurious by the excellence and variety of the food (which included a huge supply of ice-cream !), and just before sunset a start was made up the mountains for "Oak Camp" where the first night was to be spent. The lowermost slopes are covered by a magnificent stand of *Carnegia* mixed with *Fouquieria*. At a somewhat higher level these disappear and the first evergreen oak (*Q. oblongifolia*) appears, with *Juniperus pachyphlœa*, *Arctostaphylos pungens*, *Dasylirion Wheeleri*, *Nolina microcarpa*, etc. The camp in "Soldiers' Canyon," nearly 5,000 feet above the sea among the evergreen oaks and accompanying sclerophyll scrub, was reached long after dark. September 22nd was spent among the vegetation of this region, which is a transition between semi-desert and sclerophyll vegetation. On the morning of September 23rd the further ascent of the range was undertaken. Among the evergreen oaks (*Q. emoryi*, *Q. hypoleuca* and *Q. arizonica*) the dwarf *Pinus cembroides* (one of the "pignon" group, close to *P. edulis* and *P. monophylla*) appears, and about 5,500 feet it increases and permeates the whole open woodland. "Manzanita Ridge" is covered with scrub among which *Arctostaphylos* spp. are conspicuous. Towards 6,000 feet the tall southern yellow pine (*P. arizonica*) comes in, and shortly afterwards *P. chihuahuaensis*. Here and there a few Douglas spruces and *Pteridium aquilinum* also appear. On the north-facing slope descending into Bear Canyon—the site of the next camp—there is a closer but still sparse wood of yellow pine with *Arbutus arizonica*, *Ceanothus Fendleri*, *Arctostaphylos Pringlei*, *Juglans major*, *Quercus Gambelii*, *Rhus elegantula*, *Berberis Wilcoxiana*, etc.

On the morning of September 24th most of the party returned to Oak Camp *en route* to Tucson and the Grand Canyon of the Colorado River, but a party from the Desert Laboratory accompanied by a few members of the international party continued the trip to Mount Lemmon on the summit of the Santa Catalina range. The south-facing side of Bear Canyon up which the route lay is a nearly vertical slope so dry and fully exposed to the sun that many desert plants go right up to the summit between the evergreen oaks and manzanita scrub. There are no pines on this face. Immediately the summit is reached, at a height of about 7,000 feet, one enters a fine open forest of *Pinus arizonica* with species of *Arctostaphylos*, *Quercus emoryi* and *Ceanothus Fendleri* as undergrowth. The trail winds through this forest round the valley sides for a considerable way, and magnificent distant views of the lower slopes and the desert are obtained. In the damper shaded valleys deciduous trees and shrubs like *Acer interior* (of the *Negundo* type) and *Alnus acuminata* occur. At about 7,800 feet the manzanitas, *Arbutus* and *Quercus emoryi* disappear and isolated trees of *Pinus strobiformis* are met with. In the pine-wood at this level a whole set of herbaceous "montane" plants are found: the beautiful *Aquilegia chrysantha* and *Lobelia Grewiana* by damp stream-sides, *Potentilla Thurberi*, *Heuchera rubescens*, *Oreolirion* (*Sisyrinchium*) *arizonicum*, *Gilia Thurberi*, with *Pteridium aquilinum* and *Achillea Millefolium*. In a north-facing canyon a thick stand of Douglas spruce with *Abies concolor* and fine trees of *Acer grandidentatum* with deciduous undergrowth indicate a still higher zone. Beyond, a flat-topped ridge, more than 8,000 feet above the sea, is traversed, with fine forest of yellow pine; and a short but steep descent brings the trail to Marshall Gulch, the last camping ground. The nights in Marshall Gulch at this time of year are very cold, a thick layer of ice being formed on the water left overnight in pails. Marshall Gulch is occupied by Douglas spruce wood; associated with the dominant are *Abies concolor* and *Pinus strobiformis*, with *Acer grandidentatum*, *Populus tremuloides*, *Alnus acuminata*, *Quercus submollis*. A rich "montane" ground-flora occurs in the wood, a majority of the forms belonging to genera also occurring in northern Europe, such as *Rubus*, *Ribes*, *Cornus*, *Silene*, *Aquilegia*, *Aconitum*, *Actœa*, *Viola*, *Fragaria*, *Agrimonia*, *Lathyrus*, *Vicia*, *Trifolium*, *Heracleum*, *Valeriana, Mimulus, Galium, Erigeron,* with a few European species —*Pteridium aquilinum, Cystopteris fragilis, Pyrola minor.*

September 25th was devoted to the ascent of Mount Lemmon and a short circuit through the woods on the north side of the main range. The southern slopes of Mount Lemmon, from 8,000 to 9,000 feet, much more exposed to the sun than the valleys like Marshall Gulch, are covered with a rather sparse wood of *Pinus arizonica,* with *Quercus reticulata, Q. hypoleuca* (evergreen), *Q. Gambelii* (a deciduous but leathery-leaved form), and *Ceanothus Fendleri.* This vegetation goes right up to the summit (just over 9,000 feet) and is very little affected by wind. On the steepest faces the pines are few and the ground is mostly occupied by oak scrub. The view from the summit of Mount Lemmon is very extensive, reaching to the Sonoran mountains in Mexico to the south, and the northern Arizona mountains leading up to the Great Colorado Plateau on the north. On the north face there is good forest of *Pseudotsuga* and *Abies concolor,* with many of the same species as in Marshall Gulch.

On September 26th the return journey was made as far as the Bear Canyon camp, where it was still very cold at night, though the thermometer did not actually go below freezing point. By mid-day on the 27th we were back on the baking desert plains with shade-temperatures of over 100°F., returning to Tucson by automobile from the foot of the mountains.

The Santa Catalina trip was in many respects the most enjoyable part of the whole tour. The restful days of riding slowly through the great pine forests in perfect weather, the glorious, ever-changing views, the fine zonation of the vegetation, the abundance of interesting plants, and the many talks round the camp fire at night with our kind and thoughtful hosts from the Desert Laboratory—these things combined to make the week's camping trip an experience impossible to forget.

NEW MEXICO AND KANSAS.

September 28th and 29th were spent in and around Tucson, and on the afternoon of the second day we rejoined the main party on their return from the Grand Canyon and travelled with them to El Paso (Texas) 300 miles to the east, on the Mexican border, where we arrived on the morning of September 30th. Here we had a few hours to spare, and walked across the dry bed of the Rio Grande into the Mexican town of Ciudad Juarez, soon afterwards the scene of much bloody fighting. The bulk of the party then continued their journey south-eastwards to New Orleans, while the writer travelled north-eastwards to Chicago by the Rock Island line, traversing the states of New Mexico, Kansas and Illinois. From El Paso (3,700 feet) to Alamogordo (4,312 feet) the country is good semi-desert, the average height of the undershrubs not being more than eighteen inches. *Yucca* and *Agave* are locally abundant, and various grasses and other herbs occur—thickly in places—among the woody plants, though at this time of year they are mostly dried up. *Gutierrezia* and an *Artemisia* were also abundant. About Alamogordo the shrubs become taller and a fine range of mountains with forest on the higher slopes is approached, and before Carrizozo (5,438 feet) is reached the grasses have become practically continuous and the woody plants, except locally, have almost disappeared. The "Great Plains" region is entered. A species of *Yucca* is still abundant locally. The hills near the railroad are scrub-covered to their base, with grassy mesas in front. The line steadily climbs, and near Largo (6,000 feet) Juniper scrub mixed with *Yucca*, *Dasylirion* and a much branched cylindropuntia is scattered thickly in the grassland. Presently a Pignon pine comes in, mixed with the scrub and forming a dwarf wood. This apparently extends over the summit of the divide, which is crossed near Corona at 6,666 feet, but darkness prevented further survey of the vegetation.

On the morning of October 1st we entered the south-western corner of Kansas, still in the Great Plains type of country. During the day as we travelled north eastwards through the state this gradually changed to the Prairie type. It is noticeable that here, just as further north in Nebraska, while the vegetation of the Great Plains is still almost entirely in a natural state, no natural prairie could be seen from the train, the land being almost entirely arable—now in stubble. Trees began to show much more luxuriant growth, and around Herington and beyond natural river-bottom woods began to appear, the cultivation stopping, again as in eastern Nebraska, with the limits of the original prairie. Around Topeka woods—largely of oak—began to appear on the hills, and further on thick woods covered the hills, the lowlands being black soil prairie, all under crops. Along this diagonal section across the state of Kansas no considerable hills are anywhere encountered, and the country is all flat or gently rolling plains with occasional low ranges. Kansas City was reached after dark, and early in the morning we crossed the Mississippi and were soon in the familiar country of the state of Illinois, reaching Chicago before noon.

AUTUMN COLOURS.

After a few days spent in Chicago the writer travelled to Boston and thence sailed for England. In the New England and adjoining states—especially in the Berkshire Hills (New York)—the autumn colours were in their full glory. The greater richness and variety of the autumn colouring seems to be due to the much greater variety of trees and shrubs as compared with north-western Europe, rather than to climatic differences. Thus there is a greater absolute number of species which show beautiful and conspicuous colours, such as crimson, rose-red and orange, than is the case in our own much poorer woody flora. The autumn in Illinois, Indiana, and in New York and the New England states was, at least in 1913, distinctly earlier than in England. The trees at Chicago had lost more leaves at the beginning of October than our own past the middle of the month, when the landscape and gardens still full of flowers showed almost a late summer aspect. There must indeed have been three weeks or even a month's difference between the seasons. This may have been partly due to the very hot American summer and the cool British summer of 1913. The spring at Boston in mid-May was certainly no more or even less advanced than that of central England at the end of April. Both these things are no doubt mainly due to the continental as opposed to our insular climate.

I cannot close this rather sketchy account of the American I. P. E. of 1913, without again trying to express the deep indebtedness of all the members of the party to our American hosts, who, one and all, did everything in their power to make our visit pleasant and profitable. Certainly no member of the international party will ever forget the overwhelming impressions we received of American landscapes and vegetation, designed truly on the grand scale, or of unrestrained American hospitality. Apart from these the most vivid impression I personally obtained was of the earnestness and single-mindedness of American science. In the vast field of ecology America has secured a commanding position and from the energy and spirit with which the subject is being pursued by very numerous workers and in its most varied aspects, there can be little doubt that her present pre-eminence in this branch of biology—one of the most promising of all modern developments—will be maintained.

ON THE RELATION BETWEEN *CYCADITES* AND *PSEUDOCYCAS.*

By Ruth Holden.

European Fellow of American Association of Collegiate Alumnæ.

[With Plate III and One Figure in the Text.]

Within the last few decades, a great amount of work has been done in the endeavour to work out the relationships of fossil Cycads. It has proved an extremely arduous undertaking, owing chiefly to the scarcity of anatomically preserved material. This is true especially of leaves, where the criteria used in classification are necessarily based on the external features perpetuated by impressions. Recently, however, numerous additions have been made to our knowledge of fossil plants through the improved technique of the eminent Swedish palaeobotanist Nathorst. Nowhere has this work been more welcome than in its application to cycad fronds, and we may now hope that our classification will be based on features which are constant and trustworthy. As extended by Thomas and Bancroft (5) to the correlation of living and fossil material. we are now able to examine intelligently such minute structures as stomata, and to understand even the details of the thickenings of the guard cells. The importance of such work cannot be overestimated and it is very desirable that these new methods will be applied wherever possible.

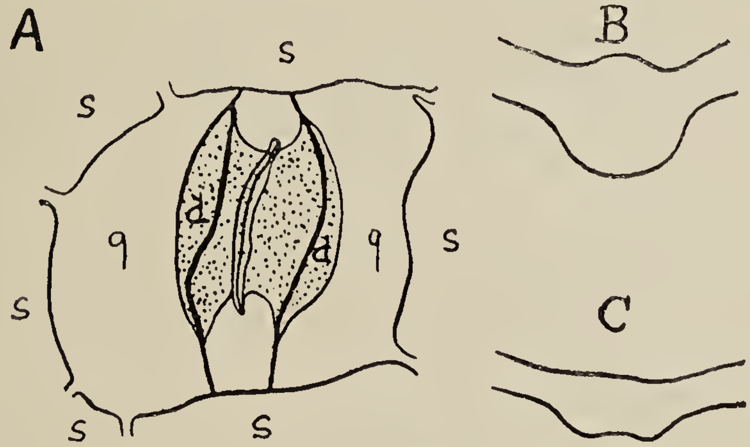
An interesting contribution by Nathorst (1) has been the establishment of the genus *Pseudocycas* for certain cycadean fronds formerly referred to the genus *Cycadites.* They differ from the latter genus in the possession of a double instead of a single midrib, and in the fact that the pinnules are not narrowed, but if anything broadened at the point of attachment to the rachis. The former character is not invariable, for *Pseudocycas Steenstrupi* has always, and *P. insignis* at times, only a single midrib—a discrepancy which Nathorst explains by suggesting that the two veins may sometimes fuse. Further, the stomata of the new genus are confined to the ridges formed by the double midrib and to the furrow between ; the epidermal cells are in long rows, and their walls are sinuous. Unfortunately the cuticle of an undoubted *Cycadites* has never been described, but assuming it to be like the living genus *Cycas,* it is evident that these constitute further points of difference, since the stomata of the latter are scattered irregularly over the entire lower surface, with the exception of that part which underlies the vein, and the epidermal cell walls, though heavily pitted, are quite straight. To clear up the relation between *Cycadites* and *Cycas*, it occurred to the writer that it would be advisable to examine the cuticles of the English specimens, and through the kindness of Dr. E. A. Newell Arber in lending material from the Sedgwick Museum, this was rendered possible.

There are two species of *Cycadites* represented in the Sedgwick Museum—*C. rectangularis* Brauns and *C. Saportæ* Sew. In the former, a Rhætic species, the presence of a double midrib is very marked but unfortunately the condition of preservation is not such that it is possible to examine the cuticle. In the latter, an English Wealden species, it is noticeable that in the impression of the lower surface there are, at places, indications of a double midrib, though usually it is unquestionably single—a state of affairs paralleled by Nathorst's *Pseudocycas insignis*. In Plate III, Fig. 6 shows a strip of cuticle from one of these specimens. To the left may be seen the midrib, the white line down the centre indicating that it is double. As in Nathorst's material, the furrow between the two ridges overlying the veins is often filled with a dark, opaque substance, difficult to clear away, which obscures the double nature. All this central region is covered with stomata. Fig. 7 illustrates another preparation at a higher magnification, and the stomata here are very plain. This second pinnule, however, has but a single midrib, though it came from the same leaf as the first. The tissue immediately to the right of the midrib (Fig. 6) represents the remainder of the lower surface, the black line slightly to the left of the centre of the photograph, being the edge of the leaf. Here the sinuous walls of the epidermal cells, and their arrangement in rows are shown to be identical with those figured by Nathorst, but an important difference is the presence of additional stomata. As noted above, they occur in large numbers down the central groove, but there are also a few others scattered irregularly to the right and left of the midrib—in Fig. 6, about ten. To the right of the central dark line is the upper surface of the leaf. In general character it is like the lower, except for the complete absence of stomata and the lack of differentiation of the tissue overlying the midrib. From this description of *Cycadites Saportæ*, it is evident that the resemblance to *Pseudocycas* is very close, the only point of difference being the additional stomata of the lower surface in the former species.

In the British Museum, there is a single specimen of *Cycadites Roemeri*, also from the Wealden of Hastings (4). From this, through the kindness of Mr. Edwards, a few pieces of cuticle were obtained, which yielded excellent preparations. Fig. 8 is a photograph of one. At the extreme left may be seen the cells overlying the midrib on the upper surface of the leaf. Fig. 9 (the same region from another preparation at a higher magnification) shows that these cells are extremely like those covering the entire upper surface in the case of *Cycadites Saportæ*, being sinuous-walled, arranged more or less in rows, and devoid of stomata. Toward the right, an intermediate zone may be seen, in which the cells have in the centre, small circular projections. These probably represent hair scars, as similar appearances have been noted by Nathorst in *Pseudocycas Steenstrupi.* The black line in the centre of Fig. 8 represents the edge of the leaf, where the upper surface was not completely separated from the lower; at the extreme right is the midrib of the lower surface. From this photograph it is evident that the whole leaf is densely covered with stomata, with the exception of the tissue overlying the midrib on the upper surface. The structure of the midrib of the lower surface is not apparent from this photograph, but examination of the preparations themselves indicates that it is identical with *C. Saportæ*, except that its double nature is not equally obvious.

In regard to the stomata themselves, they are so similar in both species that they may be advantageously considered together. As pointed out by Thomas and Bancroft (5), there is a general Cycadean type of stoma which varies but slightly in all living and fossil forms. Among the variable features, may be mentioned number of accessory cells, shape and size of guard cells, etc. Between extant and extinct, however, there is a further point of difference, dependent on the fact that in the former the xerophytic habit has caused an almost universal sinking of the guard cells with the consequent interposition of one or more series of intercalary cells between them and the accessory cells proper while in the latter, at least in the Bennettitales group, the stomata open directly on the surface. In Fig. 10, the structure of a few stomata of *Cycadites Roemeri* is shown; Text-Fig. 1A represents another at a higher magnification. If these be compared with Thomas' figures of *Anomozamites*, *Iaeniopteris*, etc., it is obvious that there is a striking similarity, and that the genus *Cycadites* should be included in the Bennettitales group.

From this description of *Cycadites Saportæ* and *C. Roemeri*, it is evident that they agree closely with Nathorst's specimens of *Pseudocycas* except in the distribution of stomata. As far as living members of the Cycadales are concerned, Miss Bancroft (5) has shown that this feature is not constant, at least within the genus. For instance, Kraus figures stomata from the upper surface of *Encephalartos Altensteinii*, though neither she nor Nestler found them in other species; Bornemann records them on the upper surface of *Zamia muricata* var. *picta*, where she saw none. In the present case, there seems to be a series from *Pseudocycas insignis* and *P. Steenstrupi*, where the stomata are confined to the midrib of the lower surface, through *Cycadites Saportæ* where a few additional ones appear scattered over the remainder of the lower surface, to *C. Roemeri* where the whole leaf is covered except for the midrib of the upper surface. Nathorst suggests that there may be some physiological connection between the boreal habitat of his specimens and the restricted stomatal area, since it is shared by *Pinus Crameri* and another conifer from the same region. If so, it is only natural that with the more genial English climate should come the enlargement of the stomatal areas. All the evidence seems to indicate, however, that the difference in distribution of stomata is not of vital importance, and favours the transference of *Cycadites Saportæ* and *C. Roemeri* to the genus *Pseudocycas*.



TEXT-FIG. 1. A, stoma of *Cycadites Roemeri* in surface view (*g*, guard-cell; *d*, dorsal thickening; *s*, subsidiary cell). B, C, transverse sections of leaf of *Cycas* sp. in the fresh state (B) and in the dried state (C).

The next question to arise is the relation of other members of the genus *Cycadites* to *Pseudocycas*. Where cuticles are unavailable, the only criterion is the double midrib. In changing *Cycadites Dicksoni* to *Pseudocycas Dicksoni*, Nathorst seems to regard that character as diagnostic in itself, and on this ground it is not impossible that all specimens of *Cycadites* may have to be transferred to *Pseudocycas*, and the former genus abandoned. Such is the case with Saporta's figures of *C. rectangularis* (2), and the specimens in the Sedgwick and British Museums confirm his description. Similarly, the midrib of *C. Lonteti* is figured as double, and in the text Saporta refers to the "deux nervures longitudinales," but concludes that this is a fake appearance, due to the condition of preservation. No comment is offered in the case of *C. Delessei*. Schenk (3) too, figures *C. Roemeri* with a double line, but refers to it as "uninerva."

In this connection, it is interesting to consider the conditions obtaining in the living members of the genus *Cycas*. Here, of course, the midrib is unquestionably single, yet on the upper surface it usually appears as a ridge, bounded on each side by a furrow. (Text-fig. 1B). To facilitate the comparison, impressions were made from both sides of the leaf, on putty. In Plate III, Fig. 1 represents the impression of the upper, Fig. 2 the lower side of a pinnule of *C. siamensis*, and it is evident that if fossilized, the former would be referred to *Pseudocycas* and the latter to *Cycadites*. As the leaves were allowed to dry, an interesting change took place. The ridge on the lower surface, which in the impression is represented by a single line (Fig. 2) collapses down the centre, forming a groove bounded on each side by a ridge. Text-fig. 1C shows a cross section of a dried leaf; Plate III, Fig. 3 its impression on putty. If, as is probable, the analogy of living with fossil holds true, it is now easy to understand that the pinnules of *P. insignis*, *P. Saportæ*, etc., have a double or a single midrib according as the impressions were made from the upper or the lower side of a fresh or a dried leaf. A careful comparison of Nathorst's Tab. 1, figs. 3 and 5 with our Figs. 1 and 3 furnishes additional evidence that this explanation is the correct one. The two grooves on the upper surface of a leaf are always further apart than the two on the lower, the reason being that those on the upper are on each side of the midrib, while those on the lower are part of the collapsed midrib itself; and looking now at Nathorst's fig. 5, where the pinnules are broken off, it is possible to see that the furrows of the upper side of the mumified plant, are more widely separated than those of the lower. We may conclude, therefore, that when it is a question of a mumified plant, there are always two grooves with a ridge between on the upper surface; and either a single ridge, or two ridges with a furrow between on the lower, according to the condition of the leaf when carbonised.

When it is a question of impressions, the upper surface shows two ridges with a furrow between, and the lower a single furrow or two furrows with a ridge between. It should be noted, however, that in some species of *Cycas*, the collapse of the midrib is much delayed, and possibly never occurs—*e.g.*, some herbarium specimens of *C. revoluta* in the Botany School, dated 1852, showed always a single ridge on the lower surface. This is illustrated in Plate III, Figs. 4 and 5—impressions of the upper and lower surfaces respectively of *C. revoluta*; slight indications of a double line may be seen in Fig. 4, but none whatsoever in Fig. 5. Further, in one species, *C. Rumphii*, where the midrib normally projects from the upper surface instead of from the lower as in other species, the collapse is necessarily on the upper surface, so that herbarium specimens show two ridges with a groove between. Enough has been said to show, that granting a close analogy to exist between *Cycadites* and *Pseudocycas* on the one hand, and *Cycas* on the other, it is impossible to consider the presence of a single or double midrib as a character of any diagnostic significance.

This brings us to the question of the difference between *Cycadites* and *Pseudocycas*, and unless the cuticles are available, it is difficult to find one. We have shown that the midrib is not reliable, and it seems decidedly doubtful how far the character of the basal attachment as described by Nathorst will hold. It is not impossible that all the Mesozoic specimens of *Cycadites* will turn out to be *Pseudocycas*. Such has been found to be the case in all the material investigated by Nathorst, and in all the English material in the Sedgwick and British Museums; further in a recent letter to Professor Seward, Professor Zeiller states that the French specimens of *Cycadites* which he has examined, belong probably to *Pseudocycas* At the same time, the difference between that genus and *Cycas* is considerable, and probably Tertiary fronds will be unearthed whose cuticular structure will show them to be directly ancestral to *Cycas*. As a possible way out of the difficulty we may suggest that in the future the genus *Pseudocycas* should include those forms whose cuticles have the structure described by Nathorst, and that *Cycadites* should be retained for fronds resembling the living *Cycas* in external appearance, but whose cuticles are as yet unknown.

SUMMARY.

1. *Cycadites Saportæ* and *C. Roemeri* should be transferred to the genus *Pseudocycas*, since they differ from the members of that genus described by Nathorst only in the distribution of the stomata.

2. *Pseudocycas* belongs to the group of Bennettitales both on the character of the stomata and on that of the epidermal cells.

3. The presence of a double or a single midrib is of no diagnostic importance.

4. The name *Pseudocycas* should be applied only to fronds whose cuticlar structure is known; others should be referred to *Cycadites*.

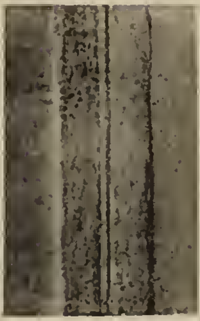
In conclusion, the writer wishes to thank Professor Seward for valuable suggestions in regard to this work; Dr. E. A. N. Arber for specimens of *Cycadites Saportæ* from the Sedgwick Museum; and Mr. W. A. Edwards for affording facilities for preparing specimens of the cuticle of *Cycadites Roemeri* in the British Museum.

DESCRIPTION OF PLATE III.

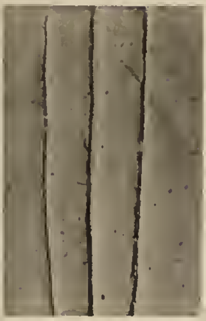
Fig. 1. *Cycas siamensis*; impression of upper surface of fresh leaf.
Fig. 2. ,, ,, ,, ,, lower ,, ,, ,,
Fig. 3. ,, ,, ,, ,, ,, ,, dried ,,
Fig. 4. *C. revoluta*; impression of upper surface of dried leaf.
Fig. 5. ,, ,, ,, lower ,, ,,
Fig. 6. *Cycadites Saportæ*; cuticle from upper and lower surfaces.
Fig. 7. ,, ,, ,, ,, lower surface of midrib.
Fig. 8. *C. Roemeri*; ,, ,, upper and lower surfaces.
Fig. 9. ,, ,, ,, ,, upper surface.
Fig. 10. ,, ,, ,, ,, stomatal area.

LIST OF REFERENCES.

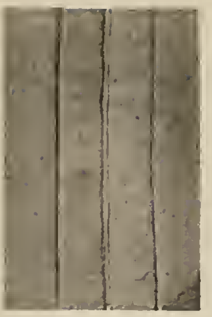
1. Nathorst, A. G. "Paläobotanische Mitteilungen. I, II." Kongl. Svenska Vet.-Akad. Handl., Bd. 42, No. 5, 1907.
2. Saporta, G. de. "Paléontologie Française. Plantes Jurassiques."
3. Schenk, A. "Fossile Flore d. Nordwestdeutchen Wealdenformation." Cassel, 1871.
4. Seward, A. C. "Wealden Flora, II." British Museum Catalogue, London, 1895.
5. Thomas, H. H., and Bancroft, N. "Cuticles of Recent and Fossil Cycadean Fronds." Trans. Linn. Soc., Bot., Vol. 8, Part 5, 2nd Ser., 1913.



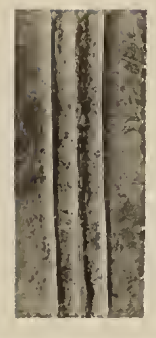
1



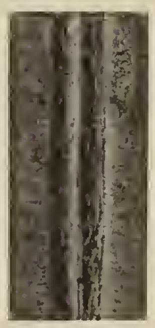
2



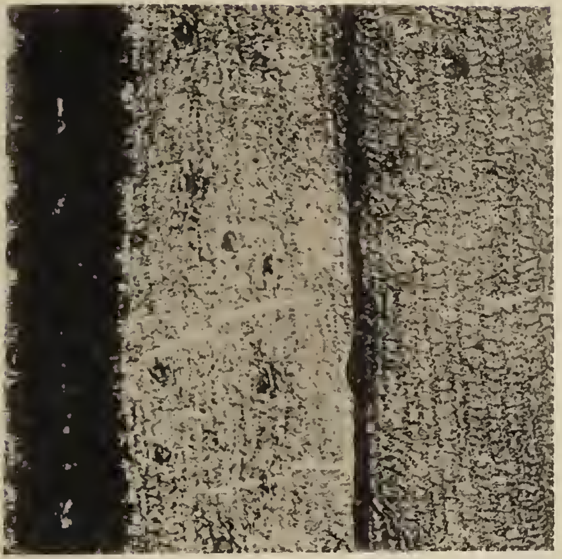
3



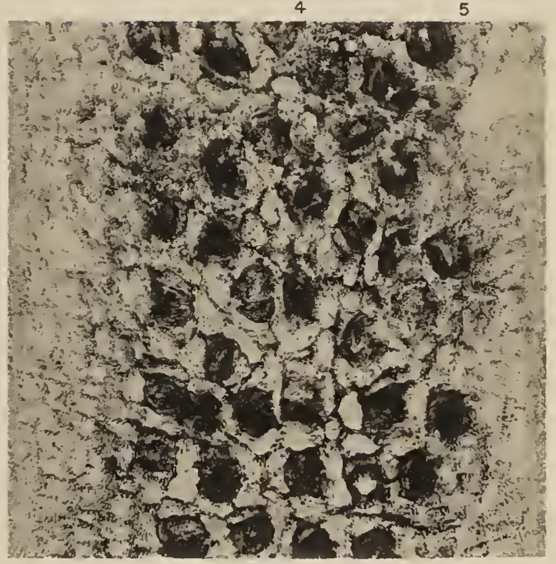
4



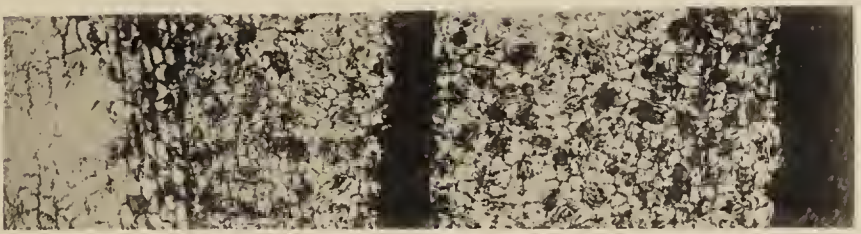
5



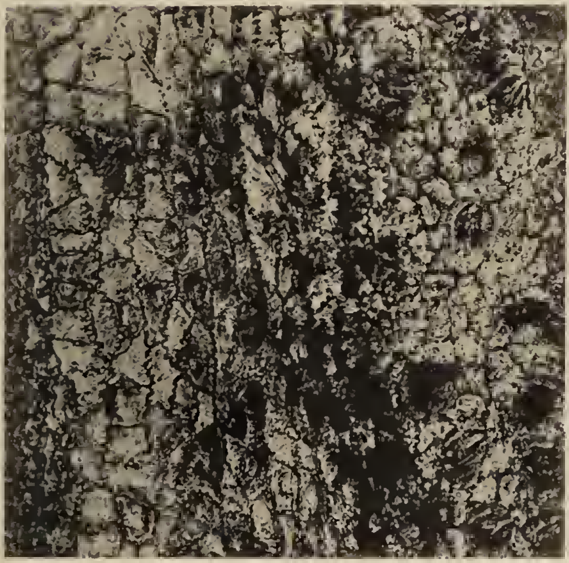
6



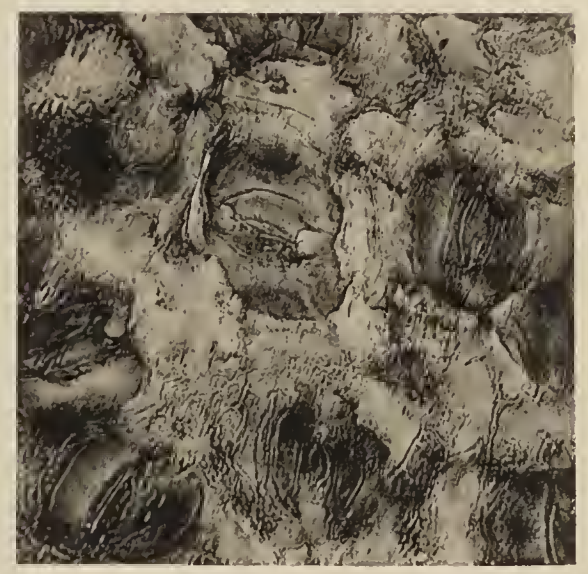
7



8



9



10

W. Tams, Photo.

HOLDEN—CYCADITES AND PSEUDOCYCAS.

FIGS. 1—5. CYCAS. FIGS. 6—10. CYCADITES.

NOTES ON BRITISH FLAGELLATES. I—IV.

By F. E. Fritsch, D.Sc., Ph.D.,

Professor of Botany, East London College, University of London.

[With three Figures in the Text.]

During the past decade the work of Klebs, Lemmermann, Pascher, and others has brought to light many new and interesting forms of Flagellata in Continental freshwaters, and a somewhat more careful sifting of our own waters from this point of view has become an urgent necessity. The present paper is a first outcome of investigations conducted with this object, and it is hoped to let others follow at short intervals.

I.—*ISOCOCCUS SPHAGNICOLUS* nov. gen. et sp. (Fig 1, A-J).

This organism was found in May in considerable numbers among *Sphagnum* in a small marsh at Keston in Kent, the only other forms associated with it being two species of *Cryptomonas* (Fig. 2, A, B), *Chrysococcus tessellatus* n. sp., *Cosmarium Cucurbita* Bréb., and numerous individuals of *Navicula.* It was placed together with some of the bog-moss in small glass vessels in the greenhouse and remained healthy, though apparently not very vigorous, for many weeks. Only certain details of the life-history have been determined, but as I am at the moment unable to obtain further material, it will be as well to give some account of what I have been able to discover as to the characteristics of this organism.

Isococcus sphagnicolus is unicellular and free-moving, except when division is taking place. The naked cell is encased in a moderately thick and smooth, colourless envelope which is spherical or frequently more oval in shape (Fig. 1, A, C); the dimensions of the envelope are 18-27μ long by 16-25μ broad, the thickness being 1·5-2μ. The envelope is separated by a narrow though clearly marked space from the protoplast except at the front end, where the latter is produced into a colourless beak from which the two equal cilia arise (cf. Fig. 1, A); I am unable to say certainly whether there is an actual connection between protoplast and envelope at this point. The cilia emerge through two distinct apertures at the anterior end of the envelope which is sometimes slightly protruded to form a very faint beak between them (Fig. 1, E); the cilial apertures are circular or occasionally slightly oval (Fig. 1, D, G), and are wide enough to allow considerable play to the cilia. Around the edge of each aperture the envelope is drawn out into a slight collar which almost invariably projects somewhat towards the outside (Fig. 1, A, B), more rarely towards the inside (Fig. 1, C). The envelope appears to be of the nature of cellulose, since it swells and takes on a violet colouration with chlor-zinc-iodide.

The actual individual within the envelope has an apparently rigid periplast exhibiting a distinct spirally twisted striation which gives the protoplast a more or less crenate or minutely dentate outline in optical section, whether viewed in the transverse or the antero-posterior plane (Fig. 1, A-D, G). Mention has already been made above of the colourless protoplasmic beak at the anterior end giving origin to the two cilia. The latter are rather more than twice the length of the whole individual and are relatively coarse, being easily seen in the living organism without the application of stains. The two cilia are identical as regards direction and mode

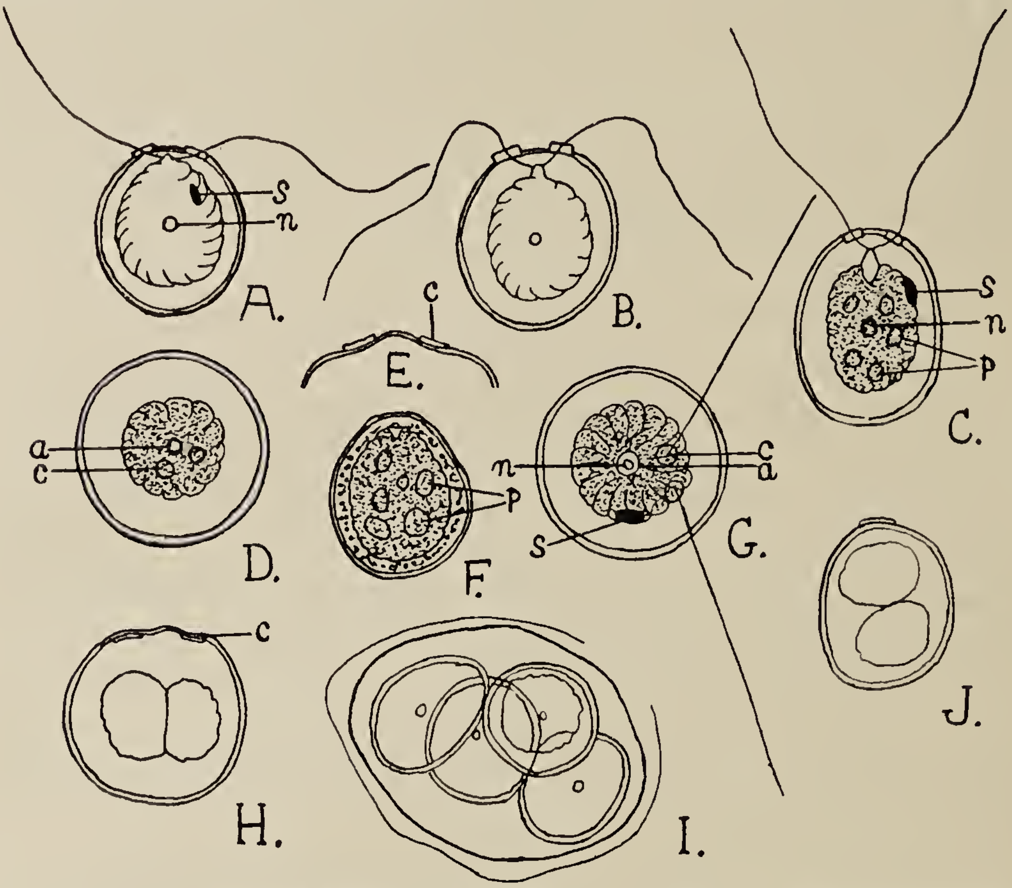


FIG. 1. *Isococcus sphagnicolus* n. gen. et sp. A, B, C, ordinary individuals (B and C after staining with Iodine) showing the cilial apertures, the spirally striated periplast, nucleus, eye-spot, and (in *c*) the pyrenoid-like bodies. D and G, oblique views of the front end, showing the cilial apertures and (in G) the aperture in the chloroplast through which the central nucleus is visible. E, small part of the anterior end of the envelope, much magnified to show the cilial collars and the small beak-like protrusion between them. F, individual with granular matter between periplast and envelope, also showing the pyrenoid-like bodies in the cell-contents. H-J, stages in division. In H the cilial apertures are still plainly visible, in I four almost mature daughter-individuals are seen. *a*, aperture in chloroplast; *c*, cilial apertures; *n*, nucleus; *p*, pyrenoid-like bodies; *s*, eye-spot. (A, H-J × 700; B, C, F × 950; D and G × 1500; E × about 2000).

of action and cause a uniform and fairly rapid forward movement combined with the customary rotation of the organism upon its own axis. I have been unable to observe any change of shape on the part of the protoplast, either in the free-swimming or resting individual.

There is a single chloroplast which is almost completely spherical possessing only a small opening at the anterior end, placed so as to face between the cilial apertures of the envelope (Fig. 1, D). In most cases the chloroplast appears minutely granular, but in some individuals it seemed to be more or less fissured, especially at the anterior end, without however actually breaking up into segments; starved specimens which had been kept in darkness for some days exhibited reticulation of the chloroplast, the actual substance being interrupted by oval or circular meshes. The chloroplast occupies practically the whole of the body, leaving only a slight colourless three-cornered or rounded area at the front end beneath the cilial beak (Fig. 1, C). The product of assimilation is starch, healthy individuals becoming almost uniformly bluish-black on staining with Iodine. Even after some days' sojourn in darkness a number of large spherical or oval bodies which become stained a dark colour with Iodine are still distinctly recognisable in the cell-contents; there are from five to eight of these bodies which appear to lie on the inner face of the chloroplast and for the most part nearer the front than the back end of the cell, but apart from that, exhibit no regular orientation (Fig. 1, C, F). In view of their persistent character and large size these structures are probably to be regarded as pyrenoids, with a closely fitting sheath of very minute starch-grains.

The small nucleus appears in all cases to occupy a central position (Fig. 1, A, B), being clearly seen through the opening of the chloroplast in individuals viewed from the front end (Fig. 1, G). The nucleus is generally quite easily visible in the living organism, but shows up very plainly after staining with safranin. A prominent eye-spot, of an elongated oval shape and appearing as a slight elevation on the periplast, is situated on one side a little way from the front end of the cell (Fig. 1, A, C, G). I have been unable to observe any contractile vacuoles.

It appears probable that there is an actual space between the envelope and the contained cell, since individuals placed in salt-solution or alcohol exhibit marked contraction of the protoplast resulting merely in a widening of the space between the latter and the envelope; in very rare cases, however, the contracting protoplasm brought to light a second boundary line internal to the envelope, as though there had been some substance, such as mucilage, between the protoplast and the envelope. I am inclined to think, however, that such cases may mark incipient division. In plasmolysed individuals the cilia are drawn back with the contracting protoplasm and their lower portions are readily recognisable on the inner side of the envelope (Fig 1, B, C); this shows how freely they can move within the cilial apertures. It should be added that in a few cases the space between envelope and protoplast was occupied by a certain amount of granular matter (Fig. 1, F).

With reference to the reproduction of *Isococcus* I am unfortunately able to say but little, all cultures with the object of elucidating certain points having hitherto proved unsuccessful. Large numbers of stages like those shown in Fig. 1, H-J were met with and I have no doubt that these represent the ordinary method of reproduction of the organism by division. This process appears invariably to take place in the resting condition and to be accompanied by a gradual widening out of the envelope; in early stages, before the latter has increased much in size, the small collars surrounding the cilial apertures are still clearly recognisable (Fig. 1, H), but in later stages these details of differentiation are lost. In all those cases, in which the point could be definitely settled, the plane of the first division of the protoplast was longitudinal (Fig. 1, H). Most commonly two successive divisions appear to occur, so that four individuals were found within the enlarged envelope of the mother (Fig. 1, I); more rarely, cases were observed in which only two individuals had been produced, whilst only once was division into eight noticed. When division into four takes place the daughter-individuals are at first ranged parallel to one another, although later their orientation becomes more irregular; in the single case noticed of division into eight, the arrangement of the individuals gave no clue to the direction of the third division-plane. In the smallest forms exhibiting division into two, the envelope measured 26μ in diameter, *i.e.*, agreed in dimensions with the largest of the free-swimming individuals; the daughter-individuals in this case measured 16μ long by 13μ wide. In many of the division-stages observed however the envelope was much wider, attaining to as much as 80μ in diameter.

In many of the stages observed, the individuals within the mother-envelope were already fully developed, exhibiting all the characteristics described above (Fig. 1, I), and it would appear as though for the most part liberation does not take place till this condition is attained. In a few cases (all observed in the late afternoon) the daughter-individuals were seen to exhibit a slow movement to and fro within the mother-envelope, the cilia of one of them being plainly visible; liberation was obviously not far off in such cases, but attempts to follow up the further course of events proved unsuccessful owing to the death of the organisms under conditions of culture. Stages were also observed in which the mother-envelope had lost its well-defined outline and was evidently becoming mucilaginous, and it is the more probable that this represents the mode of liberation of the daughter-individuals as empty envelopes from which the latter might have escaped by splitting were never observed. From all this it appears safe to assume that reproduction of *Isococcus* takes place by division in the resting condition, the planes of the first two divisions at least being longitudinal and the fully-developed daughter-individuals becoming free by gelatinisation of the envelope of the mother. Most division-stages were always observable in the morning, so that division probably takes place over night, the products being liberated towards the end of the following day.

In a few cases very small (diameter 12μ) individuals of *Isococcus* were encountered in active movement, but provided only with a very delicate envelope. These probably represent products of recent divisions that have been liberated prematurely before they were fully differentiated; in all other respects they agreed with the normal organism. It appears as though the young individuals are more commonly oval than spherical, but that they tend to assume the latter shape as they increase in size, since a considerable percentage of the larger specimens are almost spherical.

As regards the systematic position of *Isococcus* the general organisation of the cell stamps it as a member of the Volvocales although the chloroplast approaches a more nearly spherical form than is usual in that group. The only green member of Volvocales with a simple envelope hitherto described, is *Coccomonas*[1], but this differs from the form under consideration in many respects—most markedly in the fact that the individual within the envelope is not naked, but is clothed by a cell-membrane. Other differences are seen in the single cilial aperture of *Coccomonas*, in the presence of a single pyrenoid in the latter, and in the fact that the envelope gets burst open after division. As a matter of fact *Coccomonas* is merely a *Chlamydomonas* which has acquired an independent envelope, whereas *Isococcus* constitutes a parallel to *Trachelomonas* among the Euglenineæ and *Chrysococcus* among the Chrysomonadineæ. Its naked protoplast places it on a lower level than *Coccomonas* and relegates it to the Flagellate side of the Volvocaceous series. Its

---

[1] Cf. Wille, in Engler and Prantl, Die natürl. Pflanzenfam. I Teil, 2 Abt., 1890, p. 40, fig. 22, M, N.

Flagellate character is also emphasised by its longitudinal division. No form provided with an envelope is however yet known among the Polyblepharidaceæ, and I am doubtful whether a useful purpose would be served by placing *Isococcus* in this family. Although one is naturally reluctant to multiply the number of families, it would perhaps be best for the present to place *Isococcus* in a family by itself, the Isococcaceæ. When further details of the life-history are forthcoming the new genus may secure another position. It is not impossible, for instance, that it may be a reduced member of Chlamydomonadaceæ which has secondarily become naked—a light in which Pascher regards Teodoresco's *Dunaliella*.[1]

II. *CHRYSOCOCCUS TESSELLATUS* N. SP. (FIG. 3, F, G).

This form occurred in the same locality as the last but was only observed in very small numbers, so that I cannot pretend to more than a scanty acquaintance with it. The envelope is colourless and spherical (about 14μ in diameter) except at the front end, where it is slightly protruded to form the small circular cilial aperture from which the single delicate flagellum projects (Fig. 3, F). The envelope is almost completely filled by the protoplast, rather more than half of which (the back half) however is occupied by a large mass of highly refractive leucosin. Anterior to this, the periplast exhibits a very characteristic tessellate structure, being provided with numerous small round densely placed sculpturings which give a very distinctive appearance to the whole front part of the protoplast (Fig. 3, F). There are two brown-coloured plastids placed symmetrically (one on either side) with reference to the cilial aperture of the envelope (cf. Fig. 3, G); these plastids are of remarkably small size and are seen through the characteristic tessellation of the periplast. No other details of the cell-structure could be determined, nor were reproductive stages observed.

Chrysococcus tessellatus is distinguished from all the species of the genus hitherto described by the structure of its periplast and the small size of its plastids. The latter feature is of special interest, as it may indicate a tendency towards reduction of plastids, such as has undoubtedly occurred in the case of other Chrysomonadineæ[2].

III. ON SOME FORMS OF *CRYPTOMONAS* (FIG. 2, A-H).

Species of *Cryptomonas* are perhaps, apart from the Euglenineæ, the commonest Flagellates to be encountered in small pieces of water.

---

[1] Pascher, "Kleine Beiträge zur Kenntnis unserer Mikroflora, I. Zur Kenntnis zweier Volvokalen." Hedwigia, Bd. 52, 1912, p. 283.

[2] Cf. Pascher, "Über Rhizopoden-und Palmellastadien bei Flagellaten (Chrysomonaden)." Archiv f. Protistenkunde, Bd. 25, 1912, p. 189; Scherffel, "Beiträge zur Kenntnis der Chrysomonadinen." Ibid., Bd. 22, 1911, p. 327.

In many cases, however, they are only represented by isolated individuals, and are not very frequently met with in large numbers.

Certain of the species of *Cryptomonas* appear to possess a very distinctive mode of progression. Speaking generally the unicellular motile type amongst the lower Algæ is characterised by a rapid rotation on its own axis during the forward movement, and the same type of motion is exhibited by some of the species of *Cryptomonas* I have had under observation. Others, however, exhibit no rotation during their movements, the individual swaying gracefully first to one side and then to the other, during each of which swaying movements it performs a half-twist so as to expose now the one flank, now the other to the observer. This type of motion was particularly observed in two forms of *Cryptomonas* from the marsh at Keston, bearing a strong resemblance respectively to *C. compressa* Pascher (Fig. 2, B), and *C. nasuta* Pascher (Fig. 2, A). It seems probable that this method of progression is related to the dorsiventrality of the Cryptomonad individual, but its occurrence in one

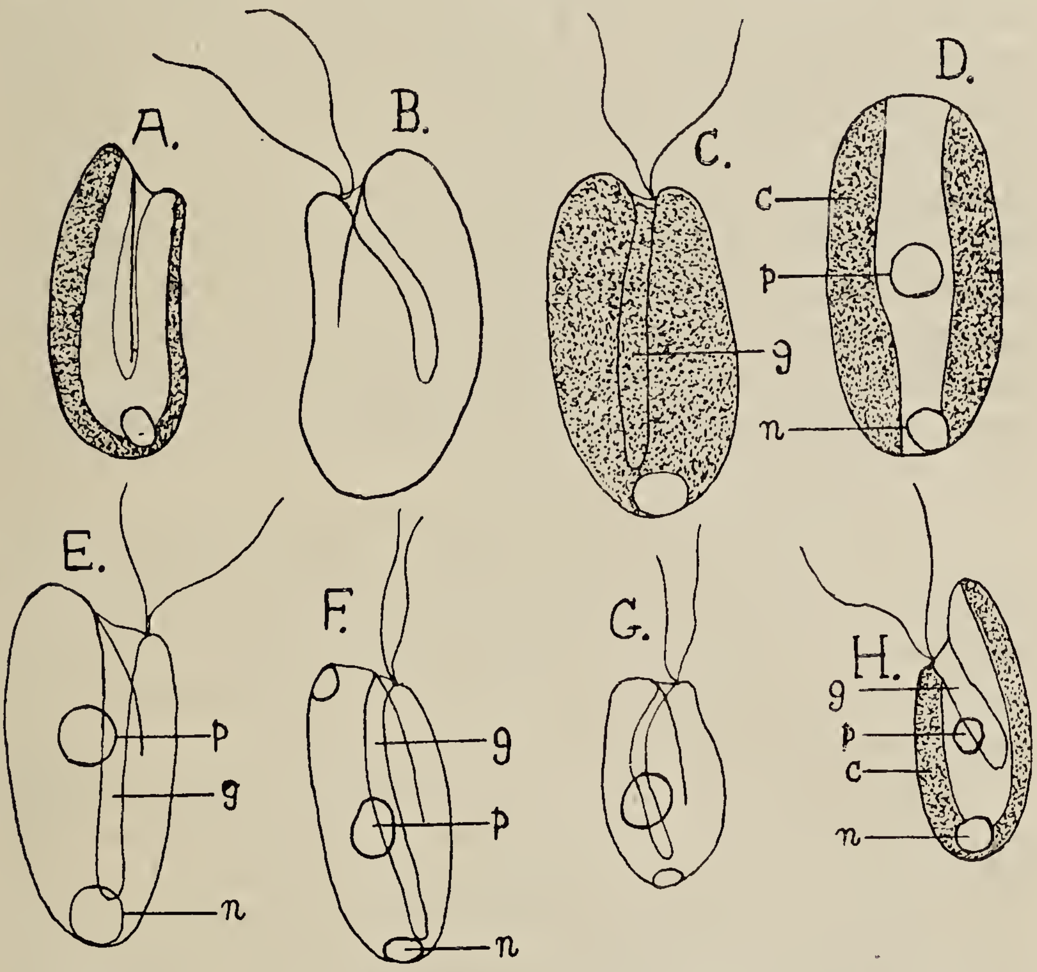


FIG. 2. Forms of *Cryptomonas*. A, form resembling *C. nasuta* Pascher. B, *C. compressa* Pascher? C-E, *C. anomala* n. sp., C and E viewed from the side, D from the dorsal surface; in C and D the chloroplasts are indicated by shading. F and G, *C. ovata* Ehrenb., forma. H, *C. Richei* n. sp. *c*, chloroplast; *g*, gullet; *n*, nucleus: *p*, pyrenoid. (A-F × about 1400; G and H × about 900).

species of the genus and not in another indicates that some special feature is probably concerned. I am, however, at present unable to offer any further data on the subject.

The commonest species of *Cryptomonas* appears to be *C. ovata* Ehrenb. I have repeatedly observed isolated individuals of this species from many localities in the neighbourhood of London, whilst a very small form appeared in large numbers in one of my algal cultures (Fig. 2, F, G). This form is 18-24μ long and 12μ broad, the cilia being about two-thirds as long as the body of the individual. The gullet is rather narrow and penetrates very deeply in most cases so as nearly to reach to the back end of the individual; it runs parallel to the body for the greater part of the length of the cell, but curves anteriorly so as to meet the emarginate front end approximately at right angles (Fig. 2, F, G). A central pyrenoid is a very prominent feature, whilst abundant starch-grains occur scattered through the cell; the bright body at the posterior end, usually regarded as the nucleus, is also plainly visible in all cases. In some individuals a second bright body, whose nature is doubtful, was observable in the anterior dorsal corner (Fig. 2, F).

The form just described differs mainly from the published figures of *C. ovata* Ehrenb. in the narrow gullet; a minor point of difference lies in the fact that the emargination of the front end is but little pronounced. It is possible that these may be characteristics of a distinct variety, but I prefer for the present to regard them as merely marking a form of the species.

I am indebted to Miss F. Rich, M.A., for some interesting material of *Cryptomonas* from Cow Pond, near Houghton-on-the-Hill not far from Leicester. I have unfortunately only seen this material in the preserved condition, and Flagellates are certainly best studied primarily in the fresh state. At least two forms of *Cryptomonas* were present; one of them (Fig. 2, H) was very scantily represented, the other (Fig. 2, C-E) in great abundance. To take the former first: it possesses characteristics which certainly seem to stamp it as new. Combined with a very marked protrusion of the dorsal anterior end, making the front edge of the organism as pronouncedly oblique as in extreme specimens of *C. nasuta* Pascher, we have a gullet whose characteristics are quite distinct. Commencing at the oblique anterior end it extends as a perfectly straight sac to the middle of the dorsal face of the organism which it almost reaches (Cf. Fig. 2, H). The cilia, which are slightly shorter than the body of the cell, arise as usual from the ventral edge of the gullet. The central pyrenoid is somewhat angular in outline. I will provisionally describe this form as *Cryptomonas Richei* n. sp., in the hope of being able to complete its description next year when living material will be available. The dimensions of the cell are 18-22μ long and 9-10μ broad.

The second species of *Cryptomonas* in Miss Rich's material is peculiar in the placing of the chloroplasts. The published figures of species of the genus invariably show the two chloroplasts on the dorsal and ventral surfaces respectively, so that both chloroplasts are visible in the side-view (when the characteristic emargination of the front end is apparent, cf. Fig. 2, A and H), whilst when the organism is seen, either from the ventral or the dorsal surface (*i.e.*, when the emarginate front end is not observable) only a single chloroplast is seen covering more or less the whole extent of the cell. In the form at present under consideration, however, the disposition of the two chloroplasts is just the reverse; they are placed laterally. As a consequence, in a side-view, the organism shows only one chloroplast and the whole cell appears uniformly tinged (Fig. 2, C), whilst when seen from the dorsal or ventral surface (Fig. 2, D) the two chloroplasts are plainly visible, one on either side. The gullet runs almost straight from the emarginate front end and nearly reaches to the posterior end of the cell (Fig. 2, C and E); both pyrenoid and nucleus are large, round and conspicuous. The cilia are markedly shorter than the body of the organism. The obliquity of the anterior end is not very pronounced, although in most individuals the dorsal edge rises to a higher level than the ventral. Reproduction takes place in the resting condition, the dividing individuals being enveloped by copious mucilage to form palmelloid groups as in other species of the genus. This characteristic form may for the present be described as *Cryptomonas anomala* n. sp., but it seems possible that the unusual position of the chloroplasts may ultimately warrant the establishment of a distinct genus. The individuals were 21-24μ long, 11-12μ broad, and 9-11μ thick.

IV.—ON TWO SPECIES OF *LEPOCINCLIS* (EUGLENINEÆ).

(FIG. 3, A-E).

In a small pond on the top of Hindhead Common, harbouring numerous individuals of *Euglena*, *Trachelomonas*, and Volvocaceæ, there occurred in some quantity a form of *Lepocinclis ovum* (Ehrenb.) Lemm., which is probably identical with var. *globula* (Perty) Lemm. (Fig. 3, C and D). The individuals are 27-30μ long and about 21μ broad, the main body being symmetrically oval with a

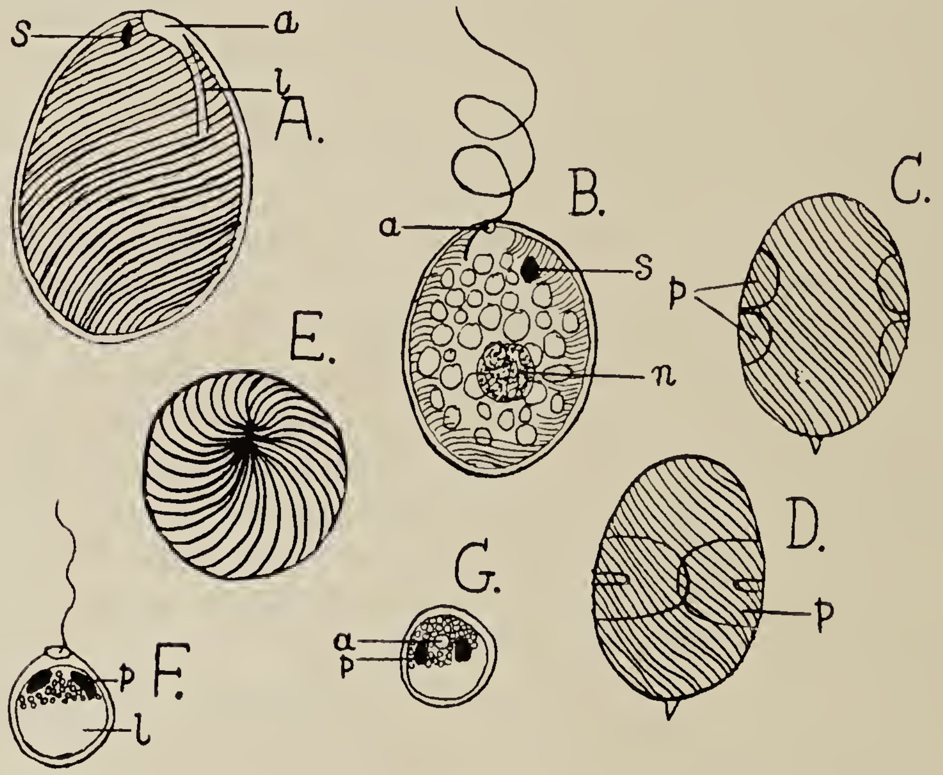


FIG. 3. A-E, species of *Lepocinclis*. A, B and E, *L. salina* n. sp. A, the periplast only; B, drawn from a living individual; E, view of periplast from the posterior end, showing the spiral striation. *a*, aperture in periplast; *l*, the superficial groove; *n*, nucleus; *s*, eye-spot. C and D, *L. ovum* (Ehrenb.) Lemm., var., to show the shape of the paramylon-bodies (*p*); C in optical section, D, from the surface. F and G, *Chrysococcus tessellatus* n. sp. F, side-view; G, view from the front end, showing the cilial aperture and the chloroplast. *a*, cilial aperture; *l*, leucosin; *p*, chloroplast. (A, C, D and E × 800; B × 650; F and G × 700).

rounded anterior end and a small pointed process ($2\text{-}3\mu$ long) at the posterior end. The periplast is provided with coarse and densely placed spiral markings, running rather steeply from the back to the front end, and exhibits a slightly yellowish tinge. Two large oval paramylon-bodies, with their edges slightly overlapping, are situated symmetrically, one on each side of the organism. Each paramylon-body is slightly drawn out in the transverse plane and takes the form of a thick ellipse, the long axis of which is partly occupied by a narrow slit; in other words, the paramylon-bodies resemble thick-walled rings which have been compressed, so that the central hollow is no more than a slit (cf. Fig. 3, D). As a consequence the cell when viewed in optical section (in the antero-posterior plane, Fig. 3, C), appears to possess four small paramylon-bodies, two on either side, and the true state of affairs is only determined by careful scrutiny. The numerous small chloroplasts, customary in the species of *Lepocinclis*, were distinct, but, since only preserved material was examined, no other details of the cell-structure could be observed. The form just described differs from the figure of *L.*

ovum given by Stein[1] in the absence of any collar at the anterior end, but since no cilium was present it is possible that the absence of the collar may have been due to contraction, subsequent to the casting off of the cilium. The process of the posterior end was also much shorter than in the form figured by Stein.

The second species of *Lepocinclis* (Fig. 3, A, B), from pools in the salt-marshes near Stanford-le-Hope in Essex, appears to be new and may be called *Lepocinclis salina* n. sp. This organism is oval, 39-45μ long by 27-31μ broad, the two ends being generally equally rounded, although the anterior may be a little pointed and the posterior occasionally bears a slight knob-like protrusion; in end-view the cell appears quite circular (Fig. 3, E). The rigid periplast is provided with a steep and well-marked spiral striation, and is extremely resistant, persisting for many weeks after the rest of the organism has died away; it becomes yellow with Iodine. At the front end of this periplast is a more or less circular aperture (Fig. 3, A, B) which is continued over the surface of the organism as a narrow groove terminating blindly about one-third of the length of the cell from the front end (cf. Fig. 3, A). From the mouth of the aperture arises the long spirally coiled flagellum (Fig. 3, B) which is about twice the length of the body and during life is in constant snake-like movement. The actual progress of this form is relatively slow, with a slow rotation of its axis, but the flagellum continues to move vigorously even when the organism is at rest. A prominent oval eye-spot is situated a little to one side near the front end (Fig. 3, A). The large spherical nucleus, readily seen in the living individual, lies a little behind the middle of the cell (Fig. 3, B). Numerous discoid chloroplasts and ovoid paramylon-bodies are scattered throughout the cell. No reproductive stages were observed. This species apparently stands rather close to *L. Bütschlii* Lemm., which has the same spiral striation; *L. Bütschlii*, however, is not so broad and is gradually drawn out at the posterior end to a point.

BRIEF DIAGNOSES OF THE NEW FORMS ABOVE DESCRIBED.

1. *Isococcus* nov. gen. Volvocacearum.

Cellulae mobiliae, nudae, periplasmate spiraliter striato, tegmine sphærico vel ovali paullo incrassato circumdato; cilia bina, plus quam duplo long. corpore cellulae, per foramina tegminis ampla bina, circularia vel paullo ovalia, collari exiguo munita emergentes;

---

[1] Cf. E. Lemmermann, "Eugleninex," in Pascher, "Süsswasserflora Deutschlands, Österreichs, und der Schweiz." Heft 2, 1913, Fig. 216 (p. 136).

chromatophora singula, fere globosa, foramine parvo ad extremum anterius, pyrenoidibus pluribus (?); nucleus centralis, stigma anterius. Propagatio subdivisione longitudinale cellulae in 2, 4, vel 8 partes in statu quiescente; cellulae filiales mox libere natantes.

I. sphagnicolus n. sp. unica. Character idem ac generis. Long. tegmin. 18-27μ; lat. tegmin. 16-25μ; crass. tegmin. 1·5-2μ.

2. *Chrysococcus tessellatus* n. sp.

Cellula parva, globosa, chromatophoris duabus parvis munita, periplasmate dimidio anteriori tessellato, tegmine sphærico foramine uno paullo exstanti, cilio uno duplo longiori quam corpore cellulæ. Diam. 14μ.

3. *Cryptomonas Richei* n. sp.

Cellula in parte dorsale valde prominens, extremo anteriori admodum obliquo, fauce recta modice lata ab extremo anteriori ad ca. medium marginis dorsalis attingente, chromatophoris duabus, pyrenoide angulari; ciliis paullo brevior quam corpore cellulae. Long. 18-22μ; lat. 9-10μ.

4. *Cryptomonas anomala* n. sp.

Cellula in parte dorsale paullo prominens, extremo anteriori modice obliquo, fauce fere recta ab extremo anteriori prope ad extremum posterius attingente; chromatophoris duabus, *in lateribus cellulæ dispositis* (non dorso et ventre ut in species Cryptomonadis typicas), pyrenoide circulari; ciliis multo brevioribus quam corpore cellulæ. Propagatio subdivisione longitudinale cellulæ in statu quiescente muco diffluenti copioso circumdato. Long. 21-24μ; lat. 11-12μ; crass. 9-11μ.

5. *Lepocinclis salina* n. sp.

Cellula ovalis, magna, extremo anteriori interdum paullo acuto, extremo posteriori interdum processu parvo munito, periplasmate rigido crasse spiraliter striato foramine parvo circulari ad extremum anterius in canalem angustum continuato instructo; cilium unum convolutum, ca. duplo longiore quam corpore cellulæ. Nucleus magnus, chromatophoræ multæ, stigma prope extremum anterius. Long. 39-45μ; lat. 27-31μ.

EAST LONDON COLLEGE,
August 27th, 1914.

A SELF-RECORDING POROMETER AND POTOMETER.

By W. Neilson Jones, M.A.

[With Seven Figures in the Text.]

I.—A Self-Recording Porometer (Figs. 1-6).

THE researches of Darwin[1] and of Lloyd[2] have emphasised the fact that variations in the rate of transpiration do not necessarily show so simple a relation with the size of stomatal aperture as was formally supposed.

It is evident that if a knowledge of the size of stomatal aperture under varying conditions is required, determinations must be made directly without reference to transpiration rates.

For this purpose two methods are in general use—(1) the alcohol method of Lloyd, (2) the porometer method of Darwin. The former has an advantage in that a *direct* measurement is made of the size of the stomatal openings; on the other hand, if successive readings are required, the porometer method of Darwin is to be preferred in that the same group of stomata remains under observation during the experiment. The estimation of stomatal aperture in this case is indirect—the unit of measurement being the time taken for a given volume of air to pass through the stomata on a given area of leaf-surface under a given average pressure. Since the results are usually required for comparative purposes, the indirectness of this method is not a serious disadvantage.

A more serious drawback to the use of the porometer as described by Darwin lies in the fact that each observation must be made and recorded by the worker—a procedure which in a lengthy experiment becomes very tedious. To overcome this drawback Balls[3] devised a self-recording instrument of very compact form and of great convenience when it is desirable to make the observations some distance from the laboratory. Indeed, the only disadvantage of this instrument—which he has called the Stomatograph—is its cost, which renders it almost prohibitive for most general laboratories.

The self-recording instrument about to be described requires only a small outlay to supplement the ordinary equipment of a physiological laboratory, and it is hoped may be of value where resources are not such as to make the acquirement of the Stomatograph possible.

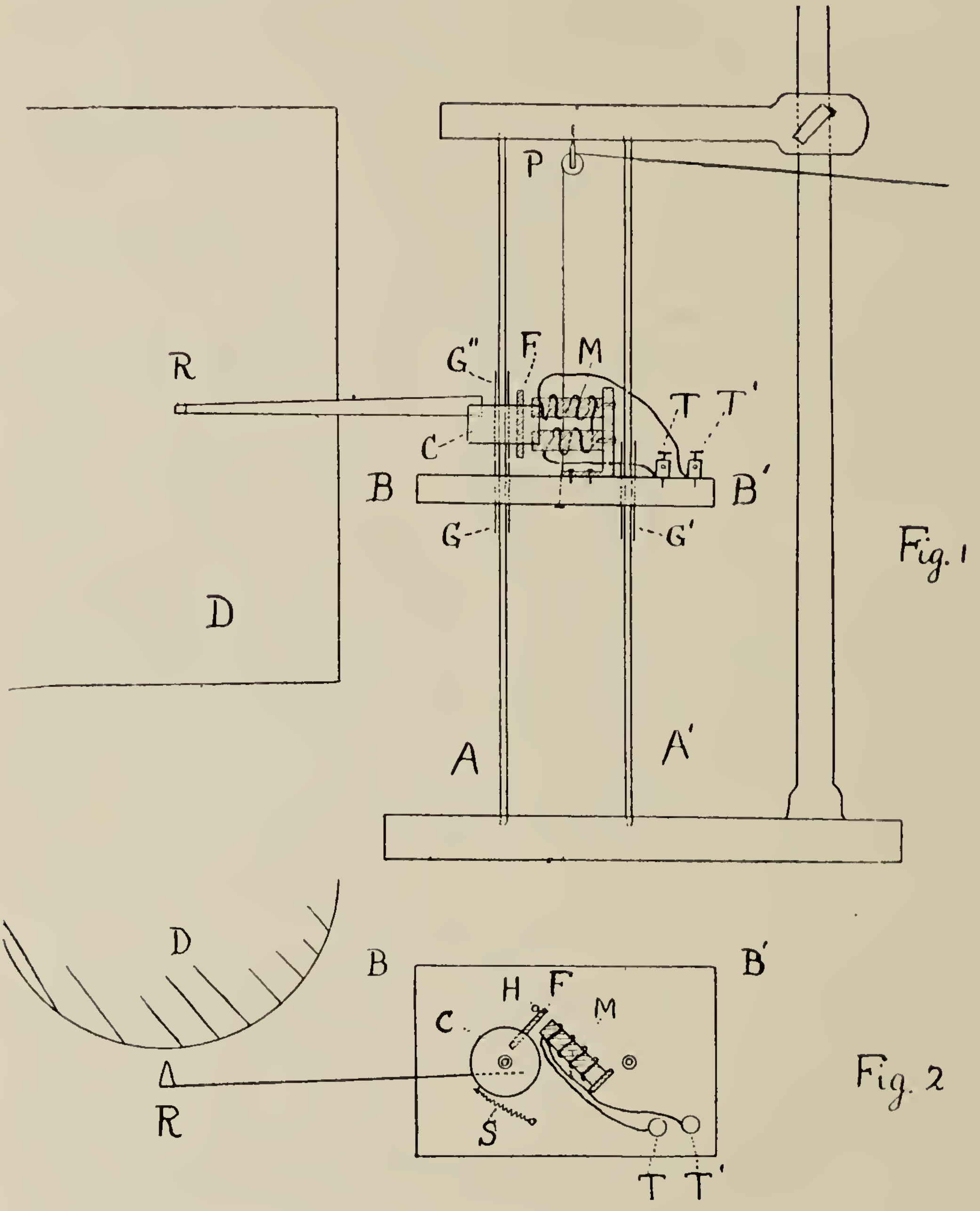
---

[1] Darwin, F., and Pertz, D. J. M. "On a New Method of Estimating the Aperture of Stomata." Proc. Roy. Soc., B, Vol. 84, 1912, pp. 136-154.

[2] Lloyd, F. E. "The Physiology of Stomata." Carnegie Inst., Wash., Publ. 82, 1908.

[3] Balls, W. L. "The Stomatograph." Proc. Roy. Soc., B, Vol. 85, 1913, pp. 33-44.

The apparatus may, for convenience of description, be considered to consist of three parts—(1) the recorder, (2) the modified porometer, (3) the driving mechanism.



Figs. 1 and 2. Self-recording Porometer. For description see text.

1. *The Recorder* (Figs. 1 and 2). The base *BB'* of the recorder may be constructed of either stout sheet cork or wood and is arranged to slide up and down two stout steel knitting needles *A*, *A'* held parallel in a wooden retort stand. To render this vertical movement as frictionless as possible, short lengths of glass tubing *G*, *G'*, of such a bore that the knitting needles will just pass through them, are fixed into the base *B B'*. This arrangement

allows of free vertical movement of the base and at the same time maintains lateral rigidity. The base is raised or lowered by a cord passing over a pulley wheel *P*. To this base is affixed an electro-magnet *M* connected to terminals *T*, *T'*. The recording pen *R* is carried at one end of a long arm of sheet aluminium, the other end of which is fixed in a slit in the cork *C*. This cork works on a glass-tube bearing *G''* similar to those in the base *BB'* and is capable of movement horizontally as well as vertically, sliding up and down with the base. Also attached to the cork *C* is a piece of soft iron *F* which functions as an armature to the electro-magnet and is kept at a suitable distance from it by a small spiral spring *S* and a stop *H* (shown in Fig. 2).

Thus, on passing a current through the electro-magnet, the cork revolves and moves forward the recording pen; when the current ceases the pen is drawn back to its original position by the spring *S*. An auxanometer drum, placed so that it is touched by the pen when in the forward position, will therefore record the periods during which a current passes.

2. *The Modified Porometer* (Fig. 3). The chief part of this apparatus consists of a glass tube some 30 cm. long and of such internal diameter that a mercury index shows no tendency to break up (2-3 mm. has been found satisfactory). At a distance of 10 cm. from each end a pair of platinum terminals are sealed through the glass (*tt* and *t't'*). The wires should project as little as possible on the inside of the tube to avoid impeding the movement of the mercury index. Towards each end the tube expands to form a slight enlargement (*b*, *b'*), the purpose of which will be described later. Having introduced an index of clean mercury about 2 cm. long, the ends of the tube are plugged with cotton wool. One end is attached by rubber tubing *r* to the surface of the leaf *l* on which the experiment is being conducted, either by the simple attachment device used by Darwin, or more conveniently by the improved form used by Balls. The rubber tubing must be long enough to allow the movement of the tube *bb'* described below. The electrical connections are evident from the diagram: the pair of terminals *t't'* are connected to the pair *tt*, and these to a cell and the recorder.

The method of working is as follows. Assuming the tube *bb'* is in the position shown and the mercury at the end *b'*, the tube is turned through 180°—until it is again vertical but with the end *b'* uppermost. The air in the tube becomes compressed owing to the weight of the mercury index and if the stomata are not completely closed, the index begins to move steadily down the tube by its own weight, the air being forced at constant pressure through the stomata. The more widely open are the stomata the more rapidly does the index move.

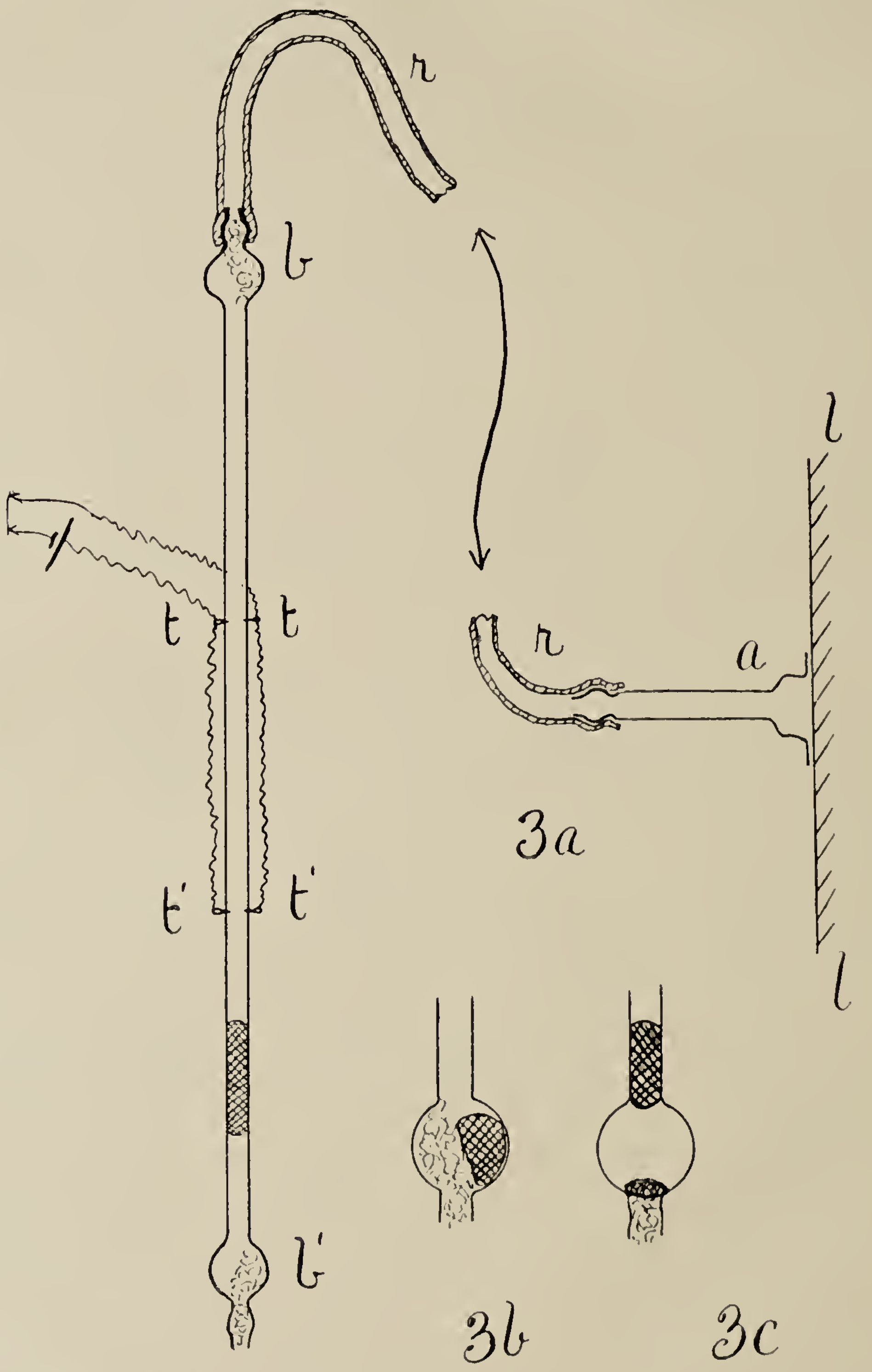


Fig. 3. Self-recording Porometer. For description see text.

As the index passes the terminals *t′t′*, the electric circuit including the recorder is completed and a record registered on the drum. A record is similarly made when the index reaches the terminals *tt*. Thus the time taken for the index to pass between the two pairs of terminals *t′t′* and *tt* is recorded on the drum. When the index has reached the lower end (*b*) of the tube, the position of tube is again reversed and another record obtained; in this case, however, air is sucked through the stomata whereas in the former case it was forced through. In this way, by reversing the position of the tube, any number of successive readings can be obtained.

The small bulbs at the ends of the tube (*b*, *b*′) are for the following purpose. It was found that if the inside of the tube was not fairly uniform in diameter where the platinum terminals were sealed through the glass, the mercury index sometimes broke in passing. The terminal bulbs allow the drops of mercury to unite should this have happened. It is important that the cotton wool plugging the ends of the tube should project into these bulbs so that the mercury can collect as shown in Fig. 3 *b*, otherwise the kind of thing illustrated in Fig. 3 *c* occurs—*i.e.*, a small blob of mercury breaks away from the index and forms a plug blocking the end of the tube. No further movement of the remainder of the mercury into the bulb takes place in consequence and the two pieces remain permanently separated. If, however, the cotton wool is pushed up one side of the bulb so as to keep the mercury to the side as it enters, this difficulty does not arise.

One other modification has been found advantageous, though not actually necessary, especially when the apparatus is required to run continuously over long periods. In order to ensure the pen writing instantaneously on coming in contact with the drum, it should strike the drum fairly forcibly. A current of voltage sufficient to ensure this, gives rise to considerable sparking at the terminals *tt* and *t*′ *t*′ on breaking contact. This leads in time to fouling of the mercury, which then ceases to run smoothly in the tube. To avoid this a relay is introduced into the circuit. A weak current is used through the tube *bb*′ and the closing of the circuit by the mercury index, instead of actuating the pen, operates the relay: this in turns starts a strong current through the electro-magnet controlling the pen.[1]

3. *The Driving Mechanism* (Figs. 4 and 5). As is evident from the above description, whenever a reading is to be taken, the tube *bb*′ must be turned upside down. In order to avoid twisting of the rubber tubing and wire connections this movement must be alternately reversed—first a turn of 180° to the right, then a turn of 180° to the left, and so on. For experiments of comparatively

---

[1] The writer uses, with suitable resistance, the electric light current for this latter. The tremulous movement imparted to the pen by the alternating current is very satisfactory from the point of view of causing immediate writing.

short duration the turning can be performed, without great inconvenience, by hand. For longer experiments an automatic turning device is desirable. The simple mechanism illustrated in Figs. 4 and 5, in connection with an intermittent klinostat, has been found to serve the purpose well.

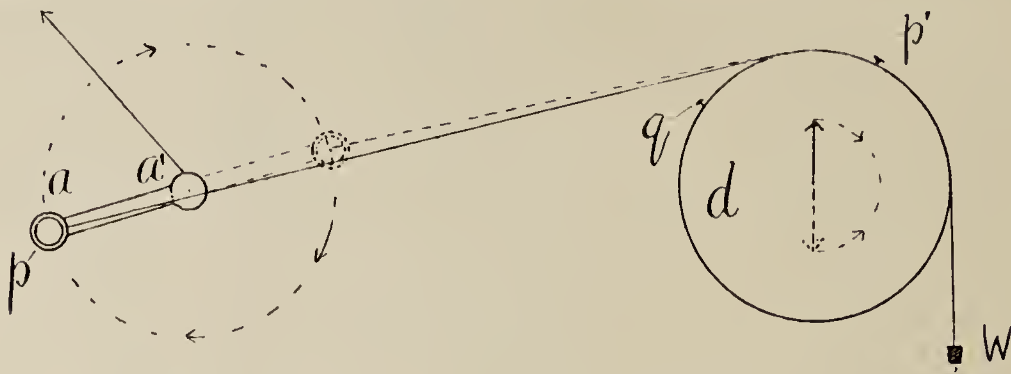


Fig. 4

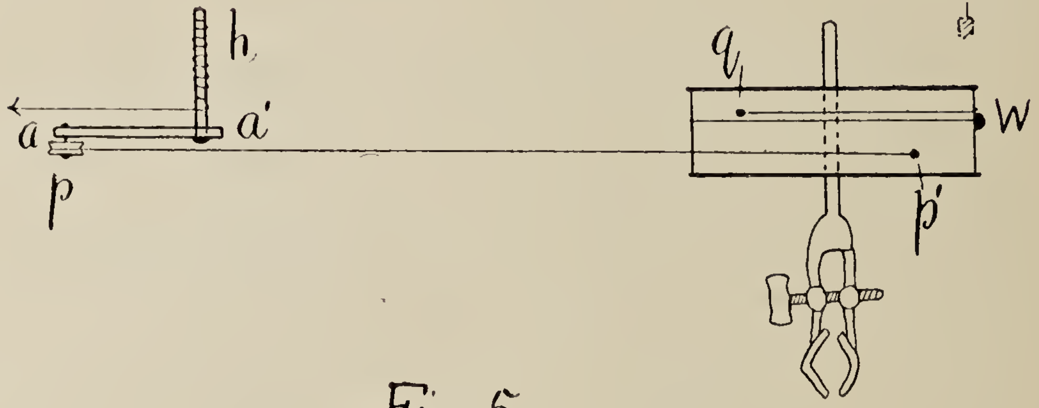


Fig. 5

Figs. 4 and 5. Self-recording Porometer. For description see text.

In Fig. 5, *h* is the driving axis of the intermittent klinostat timed to revolve through 180° once every hour. To this axis is affixed an arm *aa'* carrying a small pulley wheel *p* at its outer end. A cord, attached by a loop to this pulley wheel, runs from it to a point *p'* on a drum *d*. Another cord is attached to the drum *d* at a point *q* and after passing once completely round the drum, is fixed to a weight *W*. The effect of this cord and weight is to keep the cord *pp'* always tightly stretched.

Thus, as the axis *h* turns successively through 180°—always turning in the same direction—the drum *d* also turns through positions 180° from one another (if the length of $aa' = \frac{\pi}{2} \times$ radius of drum *d*), but first in one direction and then in the reverse back to its original position. The axis of the drum *d* is conveniently constructed of a retort clip by which the tube *bb′* of Fig. 3 is held. Lastly, the axis *h* of the klinostat (which should be 2 mm. to 3 mm. in diameter) has wound round it a cord which, running over the pulley wheel *P* (Fig. 1) supports the base *BB′* of the recorder.

Every hour, therefore, as the axis *h* of the klinostat makes a half revolution, the base *BB′* of the recorder is lowered about ·5 cm. If the recording drum is revolving once an hour, this will mean that each record of the porometer will begin on a fresh line ·5 cm. or so below the previous record. With the usual sized drum, continuous records for some thirty hours may be taken before it becomes necessary to renew the record-paper on the drum.

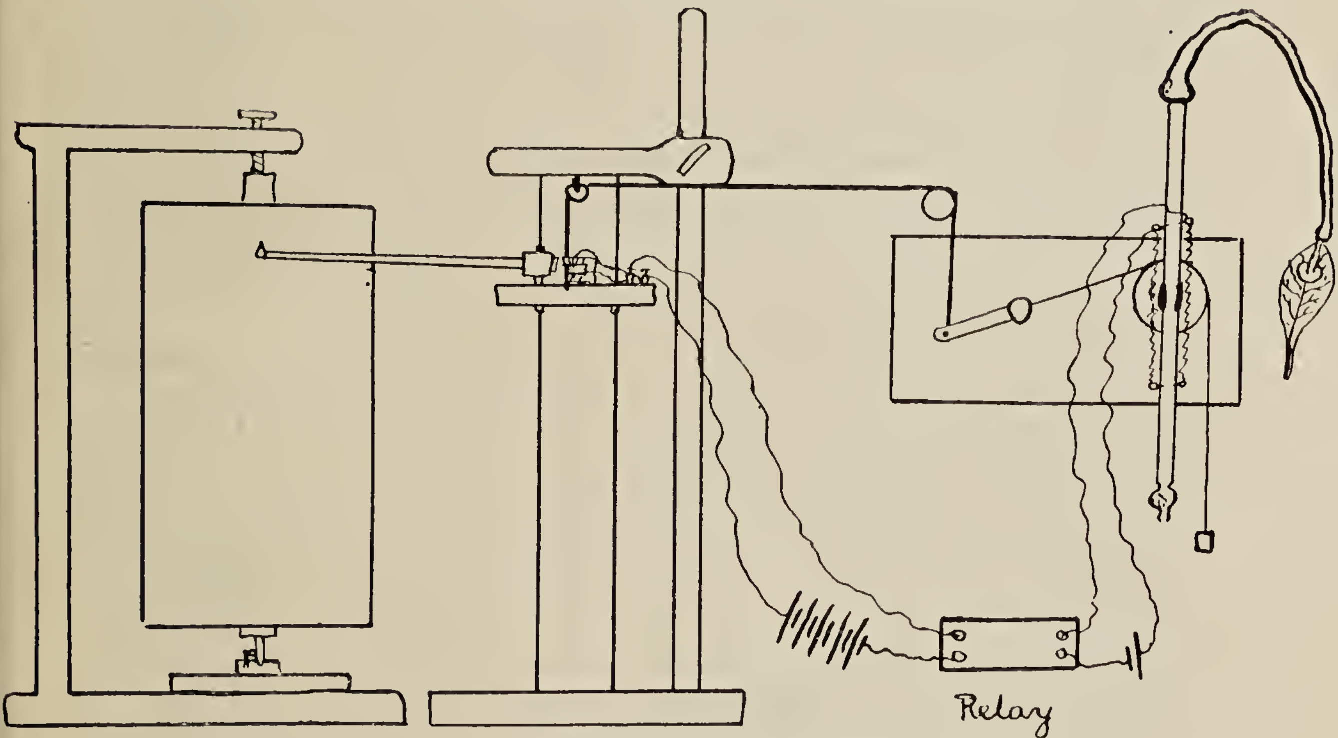


FIG. 6. Self-recording Porometer. For description see text.

The general arrangement of the component parts of the apparatus is illustrated diagrammatically in Fig. 6.

II.—A SELF-RECORDING POTOMETER (FIG. 7).

Rate of water-loss, as distinct from transpiration proper,[1] is usually measured (1) directly, by weighing a plant at intervals, (2) indirectly, by means of the potometer. A self-recording instrument of the former type has been described recently.[2] The potometer is specially convenient when the loss of water that has to be measured is small in quantity; none of the forms of potometer in ordinary laboratory use, however, is self-recording. The self-recording type of apparatus now to be described has been found to work satisfactorily and can be used in conjunction with the recording porometer.

---

[1] Darwin, F. "On a Method of Studying Transpiration." Proc. Roy. Soc., Vol. 87B, 1914, p. 269.

[2] Blackman, V. H., and Paine, S. G. "A Recording Transpirometer." Ann. of Bot., Vol. 28, 1914, p. 109.

For convenience of description it may be considered to consist of the following parts—(1) the recorder, (2) the potometer-tube, (3) the valve, (4) the electrical control.

1. *The Recorder.* The recorder described above for the recording porometer is used without modification. If the two pieces of apparatus are required for use simultaneously, a duplicate recorder must be set up.

Some means of lowering gradually the base of the recorder must be adopted—such as allowing its supporting cord to be slowly played out from a drum attached to a klinostat—so as to prevent overlapping of the record.

2. *The Potometer Tube.* This consists of a straight length of tubing BB' of about 1 mm. bore the ends of which are bent up and fused to short lengths of tubing of wider bore (3-4 mm.) AB and $A'B'$. The whole tube has the form shown in the figure. Platinum terminals are fused into the tube BB' at tt and $t't'$.

3. *The Valve.* A T-piece $CC'D$ (CC' being of wide bore tubing) has a rubber cork with a small central hole fitted firmly into the lower end C'. A long piece of glass tubing EE' of a diameter too large to pass through the hole in the rubber cork at C', has the lower end at E' drawn out to a much narrower diameter: this narrowed portion fits loosely into the hole in the rubber cork at C'. At F, on the tube EE', is fixed a rubber cork connected with the T-piece CC' at C by a piece of thin black rubber tubing. This tubing must be thin walled and readily stretched: the attachment to the cork F may be made secure by binding with wire. The upper end of the tube EE' leads to a reservoir K.

The lower end C' of the tube CC' is joined to the end A of the potometer tube by means of a piece of rubber tubing: while the side arm D is joined to the end of the potometer tube by means of the T-piece G and rubber connections shown in the diagram.

To the open end of G the experimental branch (or plant) is attached by an arrangement such as that shown at H. A mercury index about 1 cm. long is introduced into the tube $ABB'A'$ and the whole apparatus filled with water. The method of working is as follows.

Owing to contraction of the stretched rubber connection between F and C, the lower end E' of the tube EE' is pressed into the hole in the rubber cork and the tube CC' consequently closed at its lower end. The water taken from the reservoir K to replace that lost by transpiration from the branch is compelled therefore to flow along the track $EE'ABB'A'GH$.

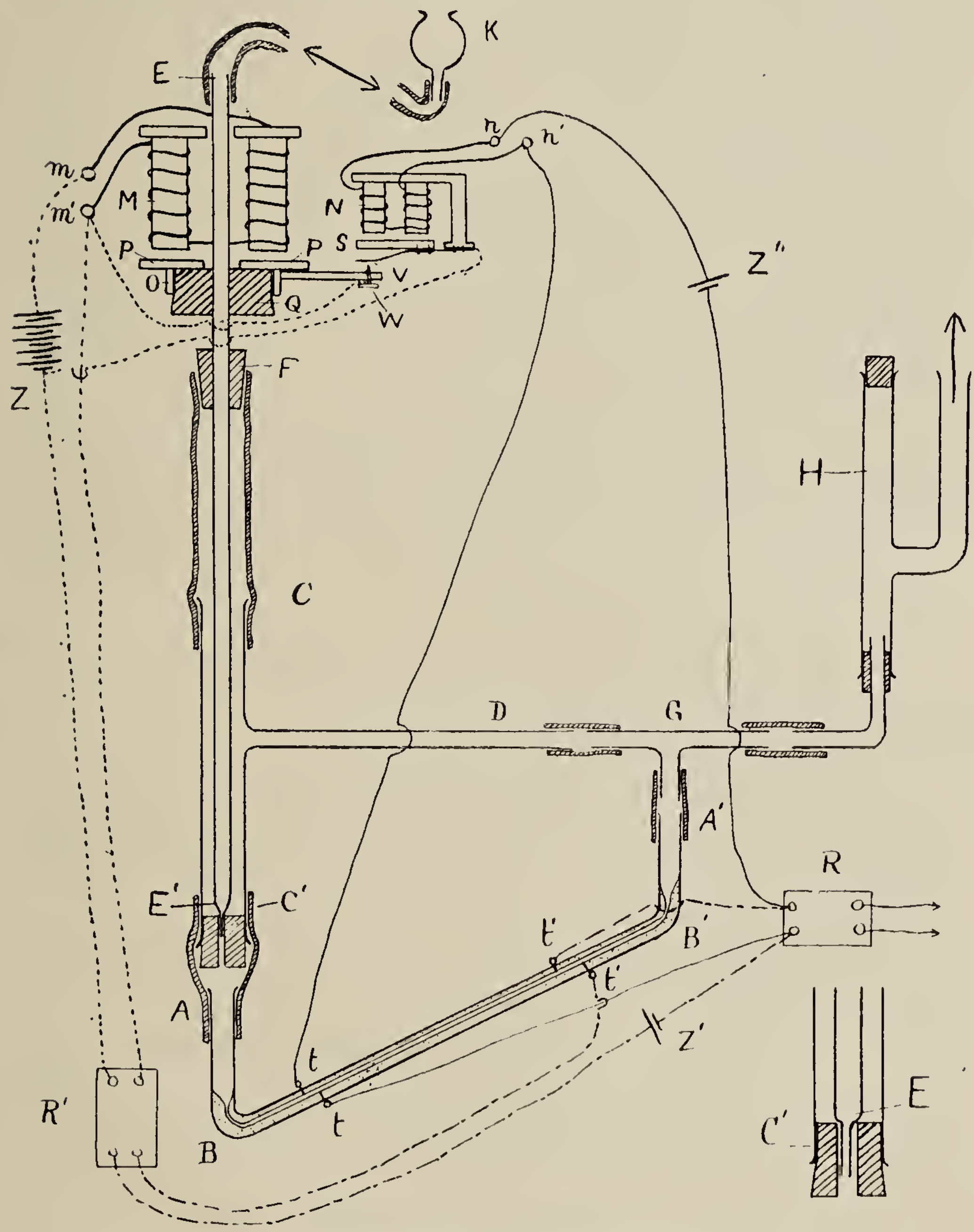


Fig. 7. Self-recording Potometer. For description see Text.

The mercury index, starting at the lowest point B of the tube $ABB'A'$, is drawn along the narrow part of this tube in the direction BB'. As it makes contact with the terminals tt (which are connected with the recorder) a circuit is established and the recording pen engages with the drum as described for the recording porometer: a similar record is made when the index reaches the terminals $t't'$.

The rate of water loss is determined by the distance between these two records on the recording drum.

If the index continues to pass up the tube BB', it reaches the wider portion $B'A'$ where it collects in a globule and the water is drawn past it: the mercury therefore cannot be drawn out of the tube $ABB'A'$.

If now the tube EE' is pulled vertically upwards so as to stretch still further the rubber tubing connecting F and C, the wider portion of the end E' is withdrawn from contact with the rubber cork closing C'. The drawn out portion of the tube, fitting loosely in the hole in the cork, serves as a guide to keep the tube EE' straight, but allows through communication between the tubes EE' or BA and the tube CC'.

The water current flowing to the transpiring branch passes now along the course $EE'C'DGH$ since by this route the necessity is avoided of moving and supporting the mercury index.

The mercury index meanwhile, being no longer supported by the "pull" of the transpiring branch, falls down the inclined tube $B'B$ until it reaches the lowest point B.

On allowing the tube EE' to return to its original position, the valve at C' closes and the mercury index once more passes up the tube BB', recording its passage as described.

Briefly—in order to cause the mercury index to return to B after it has run its course towards B', it is only necessary to momentarily open the valve at C' by exerting a slight pull upwards on the tube EE'.

There remains to be described the automatic arrangement for effecting this object.

4. *The Electrical Control.* A sufficiently powerful electro-magnet M is fixed in the position shown, the tube EE' passing through a hole in the iron plate connecting the two bobbins at the top.

The iron plate P, which forms the armature of this magnet, has an opening in the centre to permit the passage of the tube EE' and is fixed firmly to it by means of a collar O and a rubber cork Q.

Thus, when a current passes through the magnet M, the tube EE' is drawn upwards and the valve at C' opened. The terminals mm' of the magnet M are joined up to a battery of several cells Z and a relay R' is inserted in the circuit. This relay R' and also the relay R in connection with the recorder are operated by a cell Z', in the event of the circuit becoming closed by the mercury index in the tube BB' reaching the terminals $t't'$.

If the apparatus is started thus arranged the following is the course of events. The mercury index passing up the tube BB', reaches the terminals $t't'$ and completes the circuit in which the cell Z is included. The relay R is therefore brought into action and a record registered: the relay R' is also affected and the valve at C' opened as described above. The mercury index then passes back towards B, when contact is broken at $t't'$ and the valve at C' closes. The mercury index is thus left somewhere between tt and $t't'$.

In order that the valve may remain open until the index has returned to the lower end (B) of the tube BB' the following device is used.

The armature P of the magnet M carries, on an arm, an adjustable screw W. A small electro-magnet N with a moveable armature S—such as is used in electric bells—is fixed so that the spring V attached to S makes contact with W when the armature P moves upwards. V is connected with the battery Z and W with the terminal m' by wires as shown.

The magnet N is included in a circuit consisting of a cell Z'', the relay R and the terminals tt.

Thus, after the valve at C' has been opened by contact of the index with the terminals at $t't'$, the mercury commences to fall back in the tube BB' as described above: but in spite of the contact at $t't'$ being broken the valve remains open owing to the establishment of the circuit through VW.

When the index reaches tt on its downward journey, the circuit containing the magnet N is completed, the armature S moves upwards and the contact at VW is broken.

The valve at C' thereupon closes and the index is in position to start a fresh record.

Despite this somewhat involved description the actual working is quite straightforward when the electrical connections are correctly made.

Briefly—(a), the electro-magnet M serves to open the valve at C' when the mercury index reaches $t't'$, (b) the contact VW serves to maintain the valve open until the mercury index reaches tt, (c) when the magnet N comes into operation and by breaking the connection VW allows the valve to close.

In addition, whenever the index passes either tt or $t't'$ a record of the fact is made on the recording drum.

If the apparatus is required to be used over long periods continuously, care must be taken to keep the reservoir K from becoming depleted of water. The usual precautions in using a potometer—use of boiled water, etc.—must of course be adopted.

The form of tracing obtained on the drum will be evident from the following considerations.

Since contact at $t't'$ is broken almost as soon as it is made owing to the opening of the valve at C', the contact of the pen is momentary and this record has the form of a dot. The mercury then falls rapidly downwards in the tube BB' and on reaching tt another dot will be recorded which will be close to the previous dot on the drum.

The valve at C' then closes but not before the mercury has time to reach B. After a short pause the index begins to move slowly up the tube, so that the contact on passing tt in this direction is a long one. This record on the drum has therefore the form of a line, the length of which depends on the rate at which the index moves, *i.e.*, on the rate of transpiration. The complete record on the drum will therefore have the form of *a line* (as the index passes tt on its way upwards) followed after an interval by *a dot* (as $t't'$ is reached) and then immediately afterwards *another dot* (as the index repasses tt on its downward journey to B). Thus ——— .. ——— .. ——— .. and so on. The rates of water loss required will be measured by the distances between the left-hand ends of the lines and the first of the dots following.

Finally it should be remembered that the voltage of the current used across the terminals tt and $t't'$ must be less than that required to decompose water, viz., 1·47 volts.

Botanical Laboratory,
Bedford College,
London.

R. Madley, Steam Printer, 151, Whitfield Street, Fitzroy Square, London, W.